

CONSERVATION BIOLOGY



Research Priorities for the Next Decade

Edited by

MICHAEL E. SOULÉ
GORDON H. ORIAN

Foreword by

P. DEE BOERSMA

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Edited by
William C. Sousa and William F. Fagan

AND PRESS

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MICHAEL E. SOULÉ AND GORDON H. ORIANIS

Society for Conservation Biology

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CONTENTS

Foreword ix

P. Dee Boersma

Preface xiii

1. Introduction i

Gordon H. Orians and Michael E. Soulé

2. Assessment and Management of Species at Risk ii

*Georgina M. Mace, Jonathan E. M. Baillie, Steven R. Beissinger,
and Kent H. Redford*

3. Human Alteration of Food Webs:

Research Priorities for Conservation and Management 31

*Fiorenza Micheli, Gary A. Polis, P. Dee Boersma, Mark A. Hixon,
Elliott A. Norse, Paul V. R. Snelgrove, and Michael E. Soulé*

4. Exotic Species and Conservation: Research Needs 59

Carla D'Antonio, Laura A. Meyerson, and Julie S. Denslow

5. Habitat Fragmentation: Consequences, Management,
and Future Research Priorities 81

Kendi F. Davies, Claude Gascon, and Chris R. Margules

6. Conservation Priorities for Soil and Sediment Invertebrates 99

Diana H. Wall, Paul V. R. Snelgrove, and Alan P. Covich

7. Oceans at Risk: Research Priorities in Marine Conservation Biology 125
Mark A. Hixon, P. Dee Boersma, Malcolm L. Hunter Jr., Fiorenza Micheli, Elliott A. Norse, Hugh P. Possingham, and Paul V. R. Snelgrove
8. Conservation Biology and the Health Sciences: Defining the Research Priorities of Conservation Medicine 155
Gary M. Tabor, Richard S. Ostfeld, Mary Poss, Andrew P. Dobson, and A. Alonso Aguirre
9. Global Environmental Change: Effects on Biodiversity 175
William H. Schlesinger, James S. Clark, Jacqueline E. Mohan, and Chantal D. Reid
10. Making Smart Conservation Decisions 225
Hugh P. Possingham, S. J. Andelman, B. R. Noon, S. Trombulak, and H. R. Pulliam
11. Ecological Restoration: A Key to Conservation Biology's Future 245
James A. MacMahon and Karen D. Holl
12. Conservation Biology Research: Its Challenges and Contexts 271
Michael E. Soulé and Gordon H. Orians
- About the Contributors 287
- Index 293

FOREWORD

AT LEAST ONE BILLION HUMANS, MAINLY IN THE RICHEST countries, currently are practicing an environmentally unsustainable lifestyle. Another billion people, mainly in the poorer countries, lack gainful employment. Both affluence and poverty cause humans to damage terrestrial and aquatic biodiversity, as well as ecosystem functioning, and modify the earth's climate. Human consumption and increasing human numbers are the driving forces behind species extinction and were the impetus for the formation of the Society for Conservation Biology in 1986.

The Society's goal is "to help develop the scientific and technical means for the protection, maintenance, and restoration of life on this planet—its species, its ecological and evolutionary processes, and its particular and total environment." After the formation of the Society, a group of scientists met to develop a research agenda for this new field, and a small book called *Research Priorities for Conservation Biology*, edited by Michael Soulé and Kathryn Kohm, was published in 1989.

Twelve years passed, and in April 2000 the Society for Conservation Biology convened a workshop funded by SCB, the Gilman Foundation, and Conservation International. Our purpose was to update the conservation biology research agenda articulated in 1989. Gordon Orians and Michael Soulé were asked to provide the scientific underpinning for priorities for research in conservation biology. Together with a steering committee, they developed the topics and invited scientists to draft papers for discussion and review. The results and insights of some of the leading conservation biologists, mainly from the United States, are encapsulated in the book before you. They will interest biologists, resource managers, and policy makers.

The open-ended agenda can and should catalyze scientific efforts, provide a meter stick to measure progress, and act as a vehicle for scientific debate. It is not meant to be a comprehensive agenda but reflects the priorities of the editors who assembled in April 2000.

Notably some trends have changed little since 1989, making many of the first book's recommendations still timely. Human uses of the land, water, and flora and fauna continue to accelerate, modifying the life support systems of many species and causing increasing numbers of extinctions. Although workshop participants made no formal assessment of progress over the intervening years, several achievements are recognized. Among the most apparent is that conservation biology is a legitimate interdisciplinary science. Its professional society is among the largest professional biological societies in the world. A more holistic approach in addressing problems and encouraging an interdisciplinary exchange of knowledge is one of the hallmarks that distinguish the field. The maturing of the discipline means that more specific recommendations and a sharper focus are possible than twelve years ago.

As president of the Society for Conservation Biology, I felt that a workshop that produced a book generated by some of the greatest conservation biologists of the twentieth century would act to renew the vigor of practicing conservation biologists and call a new generation of scientists into service for the twenty-first century. Society must increase funding for conservation biologists to gather the scientific information needed if we are to make intelligent decisions on the use of the earth's biodiversity.

Information for conservation problem solving is still in short supply. A major challenge is to identify and learn the distribution, abundance, natural history, and population trends of earth's species. Such a goal is more ambitious and more important than curing cancer, identifying the human genome, going to the moon, or living on Mars. It is a goal on which human society as we know it depends, because the richness of the services life provides—cleaning our air and water, growing our food, and, most important, giving meaning to our lives—depend on biodiversity.

The earth is small, and the creatures that share our planet remain little known. Conservation biologists must provide insights not only into what makes the tapestry of life but also into how we can maintain it, support it, and enrich it while using its services to support human life. Conservation biologists must provide much of the knowledge and help society to use it wisely. If we fail, human life will become more impoverished as species after species is exterminated and the fabric of life unravels. Can we use our knowledge to minimize our damage to the earth while we struggle toward a more sustainable path? Information, in and of itself, is not enough; informa-

tion must reach the right audience so it can be used, further refined, and developed for maximum impact, much like the headwaters of a stream pick up force and sediment to be deposited as a rich and productive delta. Ideas, like water, should be purified, renewed, recycled, and reused.

The Society has launched a magazine to use stories as a way of conveying the successes and failures of practicing conservation biologists. Stories can portray old ideas in new ways and give new ideas a context and an application not readily apparent at first glance. *Conservation Biology in Practice* is designed to build strategic partnerships to bridge the gaps between conservation practice, theory, and policy and to help humans solve the problems they have created. The two-pronged approach of identifying our scientific needs in a book and providing the vehicle of a magazine to communicate with practitioners and policy makers is one that the Society hopes will increase our effectiveness.

The book before you sets forth a research agenda for conservation scientists of all ages. It should inspire conservation biologists addressing new as well as long-established problems. Orians and Soulé have brought together a group of authors who set forth an agenda for many lifetimes of work.

P. Dee Boersma

PREFACE

CONSERVATION BIOLOGY IS A YOUNG SCIENCE THAT WAS BORN as one response of the scientific community to the current massive environmental changes occurring on Earth. Some of these alterations are threatening the existence of a significant fraction of Earth's millions of species and affecting the evolutionary processes that generate new species. The main tasks of conservation biology are to provide the intellectual and technical tools to enable society to anticipate, prevent, and reduce ecological damage, and to generate the scientific information on which effective conservation policies can be designed and implemented.

1988 Conference

As part of an effort to evaluate the status of the field and to identify major, compelling research priorities in conservation biology, experts from many fields met for three days in Florida in April 1988 (Soulé and Kohm 1989). Their discussions were motivated by the recognition that research by conservation biologists and scientists in related fields had already provided managers and planners with important information and planning guidelines. They already knew that merely setting aside samples of ecosystems often fails to achieve its intended objectives and may have unexpected undesirable outcomes if underlying ecological processes are not understood. Recent scientific insights derived from the study of patch dynamics, edge effects, population viability analyses, ecosystem processes, scale and dynamics of disturbances, invasive exotic species, patterns of endemism, and human-induced environmental changes were providing new guidelines for effective conservation and management policies. Thus, the participants in the workshop were well-aware of the potential utility of well-focused future scientific research.

The 1988 workshop concentrated on identifying priority areas for scientific research for the subsequent decade. Although participants identified many important research topics, they agreed that the following five areas were of highest priority (Soulé and Kohm 1989):

1. *Conduct a crash program of extensive surveys and mapping to identify areas that are critical for the protection of natural and genetic resources because of their high biotic diversity, or high levels of endemism, or because of imminent destruction of critical or unusual habitats and/or biotas.* Although much survey work has been done, this task has not been completed. Rapid environmental assessment methods have been developed, and surveys have been conducted in many poorly known tropical areas (Mittermeier and Forsythe 1997). Most terrestrial areas of unusually high diversity and endemism of vertebrates and vascular plants have been identified, but distributions of terrestrial invertebrates and marine organisms are still poorly known. Enough is known to demonstrate that surveys of limited taxonomic scope are often poor guides to the distribution of species in other taxonomic groups (Heywood and Watson 1995).
2. *Establishment of a small number of research sites in the tropics to develop a coordinated program of comparative research on populations, communities, and ecosystems in relatively undisturbed and secure situations.* Since 1988 the number of tropical field stations has grown, and long-term data sets have been generated at some of them. Comparative results from the four premier neotropical field stations have been summarized in the book *Four Neotropical Forests*, edited by Alwyn Gentry (1990). Volumes synthesizing research results have been published for La Selva, Costa Rica (McDade et al. 1994), and Barro Colorado Island (BCI), Panama (Leigh et al. 1982). A steady stream of publications is emerging from the Station de Recherches des Nouragues in French Guyana (Charles-Dominique 1977, 1986). Nevertheless, coordination of research themes among tropical field stations is still very poor, and no consensus has been reached on a common set of research questions that should be pursued at all stations. Therefore, although cooperation among researchers at La Selva and BCI is increasing and more and more scientists are gaining research experience at both stations, a comparative science of tropical biology has yet to emerge. Long-term research in tropical marine systems is still minimal, the few exceptions being coordinated regional programs, such as CARICOMP in the Caribbean (Ogden and Gladfelter 1986).
3. *Conduct studies at all spatial scales to assess the kinds, mechanisms, and magnitudes of impacts on ecological systems.* Since the 1988 workshop,

there has been increasing recognition of the importance of research at a variety of spatial and temporal scales, especially at spatial scales larger than those that have typified ecological field experimentation (Kareiva and Anderson 1988). Conservation biology concerns have stimulated research into metapopulation models, source-sink population dynamics, and mechanisms and patterns of dispersal, and they have highlighted the importance of long-term studies of contemporary and paleoecological data for detecting and interpreting temporal patterns of change. Thus, this research agenda is as important today as it was in 1988, and it is expected to continue to be an arena of active investigation in both marine and terrestrial systems.

4. *Enhanced support for research that focuses on the physiology, reproduction, behavior, ecological interactions, and viability of individuals, populations, and species, especially with regard to species of critical ecological or economic importance.* Although research into these important issues continues unabated today, enhanced research support has not been forthcoming. For example, the rapidly increasing sophistication of population viability analysis, its penetration into governmental agencies and nongovernmental organizations, and its recognition by the disciplines of ecology and genetics as a legitimate area for scholarly pursuit constitute one of the success stories of conservation biology; yet funding agencies still resist supporting this field, in part because it resides at the interface between basic and applied research. Fortunately, a recent initiative by the U.S. National Science Board may eventually result in increased funding for environmental sciences by the National Science Foundation (NSF 2000).
5. *Increased training for both basic scientists and natural resource managers, particularly in tropical developing countries.* There have been encouraging developments in this area since 1988. The Organization for Tropical Studies has significantly expanded its course offerings for Latin American students, both graduate and undergraduate, and it has initiated courses in Brazil and Peru to supplement its effective educational program in Costa Rica. A consortium of European universities has established an educational program in Africa, and an increasing number of North American universities sponsor tropical field courses. The World Wildlife Fund–U.S. has developed a program of Russell Train Fellowships that supports promising young tropical scientists for varying periods of time at North American universities. Encouraging though these developments are, the need identified in 1988 is far from being met. Indeed, the need is probably greater today than it was a decade ago, in part because the status of parks and similar protected areas is lower today than at any time since the Second World War, and

also because governments can now allow such protected areas to languish without much fear of criticism or adverse consequences. Training of marine conservation biologists and resource managers in tropical developing countries is still inadequate.

Current Needs

While the major tasks identified at the 1988 workshop are being addressed, new needs have arisen because of the major increases that have taken place in human activities during the ensuing twelve years. During that interval the human population has grown from four billion to more than six billion, and it continues to increase. In addition, global commerce has dramatically increased. The budgets of the major international corporations now dwarf the budgets of the governments of most countries. Lowering trade barriers that encourage trade in commodities results in major expanses of land being devoted to the production of agricultural, aquacultural, horticultural, and forest products. Conservation activities now take place in a more crowded and more intensely interconnected planet.

Thus, although it is clear that the top-priority research topics identified by workshop participants in 1988 remain on the high-priority agenda, in 2000 leaders of the Society for Conservation Biology judged that it was time for the conservation biology research community to take a fresh look at research accomplishments and needs and to offer suggestions and guidance to researchers and private and public funders for the first decade of the twenty-first century. Accordingly, twenty-six experts from four countries met at White Oak Conference Center, Florida, April 12–16, to do for the new decade what the previous workshop did for the last decade.

To foster a rapid and comprehensive assessment, ten major topics were identified by a steering committee. They are captured in the chapters of this book. One or more experts on each topic agreed to prepare discussion papers prior to the workshop, and each paper was reviewed by a respondent. Significant contributions by other participants are signaled by their inclusion as coauthors of the respective chapters, but all participants contributed to all chapters of the book.

The audience for this book includes scientists, resource managers, and funding agencies throughout the world. Because threats to biodiversity operate worldwide, success in the protection of nature for its own sake and for the sake of future human generations will require the efforts of dedicated people everywhere. Although this report focuses on the research that is most urgently needed to support wise management decisions, we recognize that research is only one component of the diverse array of activities that must be a part of the successful conservation effort. Indeed, the research we recommend would be of little value in the absence of a cadre of practitioners will-

ing and able to use the research results and insights to further their activities on the ground.

ACKNOWLEDGMENTS

Members of the international steering committee that selected the ten topics for which invited papers were requested and identified authors and respondents were P. Dee Boersma, president of the Society for Conservation Biology; Reed Noss, president-elect of the Society; Sandy Andelman; Julie Denslow; Gustavo Fonseca; Jane Lubchenco; Georgina Mace; Scott Mills; Gordon Orians; Hugh Possingham; John Robinson; and Michael Soulé. We wish to thank P. Dee Boersma, Douglas Bolger, Carla D'Antonio, Jack Ewel, Scott Mills, Joshua Schimel, and John Terborgh for their review of particular chapters.

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LITERATURE CITED

- Charles-Dominique, P. 1977. *Ecology and Behaviour of Nocturnal Primates*. New York: Columbia University Press.
- Charles-Dominique, P. 1986. Interrelations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds, and bats in French Guyana. pp. 119–135 in A. Estrada, and T. H. Fleming (eds.), *Frugivores and Seed Dispersal*. Boston: W. Junk.
- Gentry, A. H. (ed.). 1990. *Four Neotropical Forests*. New Haven: Yale University Press.
- Heywood, V. H., and R. T. Watson (eds.). 1995. *Global Biodiversity Assessment*. Cambridge, England: Cambridge University Press.
- Kareiva, P. M., and M. Anderson. 1988. Spatial aspects of species interactions: The wedding of models and experiments. In A. Hastings (ed.), *Community Ecology*, pp. 38–54. New York: Springer-Verlag.
- Leigh, E. G. Jr., A. S. Rand, and D. M. Windsor (eds.). 1982. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes*. Washington, D.C.: Smithsonian Institution Press.
- McDade, L. A., K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (eds.). 1994. *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. Chicago: University of Chicago Press.
- Mittermeier, R. A., and A. B. Forsythe. 1997. Setting priorities for biodiversity conservation: One organization's approach. In G. K. Meffe and C. R. Carroll (eds.), *Principles of Conservation Biology*, pp. 141–142. Sunderland, Mass.: Sinauer Associates.
- National Science Foundation. 2000. *Environmental Science and Engineering for the 21st Century: The role of the National Science Foundation*, NSB00-02. Washington, D.C.
- Ogden, J. C., and E. H. Gladfelter (eds.). 1986. *Caribbean Coastal Marine Productivity*. Paris: UNESCO.
- Soulé, M. E., and K. Kohm. 1989. *Research Priorities for Conservation Biology*. Washington, D.C.: Island Press.

INTRODUCTION

Gordon H. Orians and Michael E. Soulé

FOR A NUMBER OF YEARS FOLLOWING ITS ESTABLISHMENT, THE Society for Conservation Biology (SCB) was the most rapidly growing professional scientific society in the world. Its expansion reflected the high level of concern among biologists, especially younger ones, about the increasing threats to the survival of millions of species, generated primarily by human activities. The continued rapid growth of the human population, combined with increasing per capita consumption of resources, is generating unprecedented demands on Earth's renewable and nonrenewable resources. Three decades ago, the greatest threat to sustainable use of natural resources was believed to be the high rate of use of nonrenewable resources. The impending exhaustion of those resources was expected to drive up prices and create serious shortages of materials. As it has turned out, technology has been remarkably successful in finding substitutes for many nonrenewable resources, reducing demands on their use and extending the estimates of the lifetimes of their effective supplies.

What has emerged instead as being of most concern are serious problems associated with unsustainable use of Earth's renewable resources. Among these vital resources are physical processes, such as rates of soil formation and the capacities of Earth's oceans, fresh waters, and atmosphere to decompose and dissipate wastes generated by human activities. Humans are exerting substantial influences on the major biogeochemical cycles of carbon, nitrogen, phosphorus, and sulfur, and on renewable biological processes, such as the dynamics of populations of Earth's biota, that is, the species whose activities generate the goods and services on which human society depends.

In addition, the opportunities generated by modern information technology that allow people to live, work, and retire in relatively remote areas are resulting in a sprawl of human residences across landscapes. For example, in many areas of western North America, major sources of income are unrelated to local resources. Thus, for example, brokers conduct their Wall Street businesses from offices in Bozeman, Montana, and internet businesses take orders from rural locations around the world. The spatial pattern of human settlements and their impacts on the environment are changing dramatically.

In addition, conservation biologists typically consider preservation of species to be an ethical responsibility. Conservation biology, together with such disciplines as medicine, is a normative science. Conservation science is employed in the service of an ethical goal, the maintenance of Earth's biodiversity. Indeed, the U.S. Endangered Species Act is fundamentally an ethical statement. It specifies appropriate behavior that is not simply a matter of economic convenience. The combination of this ethical stance with the estimated current high rates of extinction of species gives a sense of urgency to the activities of conservation biologists. This sense of urgency influenced the selection of research priorities identified by participants during the workshop at the White Oak Plantation in Florida, April 12–16, 2000.

The Role of Basic Research

The goal of conservation biology is to provide sound scientific concepts and data to inform the design of effective conservation management actions. Recovery and maintenance plans for species are most likely to be successful if they are based on detailed knowledge of the life history traits and habitat requirements of those species. Ecosystem management should be based on knowledge of successional patterns; responses of vegetation to different types of disturbances; and responses of marine communities to changes in ocean currents, temperatures, and chemical composition. The design of systems of reserves should be based on information about the needs of species with the largest spatial requirements, locations of migration corridors and rare community types, distribution patterns of existing vegetation types, and patterns of dispersal among habitat patches. Restoration of degraded ecosystems requires information on interactions among species, the legacies of past perturbations, and the nature of continuing forces that impinge on the systems.

Thus, conservation practitioners need information on how ecological systems work, how the interactions among species determine the functional properties of the systems, and the spatial and temporal scales at which they operate. They need to know how much of what kinds of perturbations eco-

logical communities can absorb, the consequences of ecosystem fragmentation, and how and why introduced species alter ecosystems.

Unfortunately, conservation is being carried out on a planet that is poorly known. Although about 1.75 million species have been described, the total number of species living on Earth may exceed 50 million. The majority of species of insects, mites, nematodes, and inhabitants of marine sediments have not been described. The geographic ranges and ecological requirements of only a tiny fraction of described species are known. Moreover, we know little about the abundances of species and even less about population trends. Conservation practitioners urgently need much better information on distributions of species, the composition of ecological communities, and the ecological requirements of the species they attempt to preserve. Practitioners could better deal with all of the issues discussed in this report if better taxonomic and ecological information was available.

Given the high rates of environmental changes, conservation biologists are motivated to devote considerable attention to research that can deliver important results quickly. In many parts of the world, opportunities to study large systems that harbor complete biotas at reasonably normal densities are rapidly diminishing or have already been lost. Species are becoming extinct in large numbers before their traits and functional relationships with other species have been determined. Natural areas are disappearing before their potential role as components of reserve systems can be evaluated, much less implemented. Therefore, the research priorities identified during the workshop and reported herein stress activities with the potential of informing decisions to be made within the next decade. Nonetheless, workshop participants fully recognized the importance of long-term data sets and research designed to elucidate ecological processes operating over long temporal scales (Soulé and Terborgh 1999).

Threats to the Generation and Maintenance of Biodiversity

Changes in the number of species on Earth at any moment in time are the result of the rates at which species are being formed and the rate at which they are becoming extinct. Averaged over hundreds of thousands of years, speciation rates have exceeded extinction rates, with the result that Earth's current biota may be richer than it has ever been. However, the general increase in species richness on Earth over evolutionary time has been punctuated by a small number of major extinction events and a larger number of minor extinction events, after which the diversity of life rebounded over the course of several million years.

The time required for speciation—the separation of one evolutionary lineage into two lineages—varies greatly. Among plants, speciation by polyploidy is very rapid; it requires only one generation to double the number of chromosomes. Because more than half of existing species of vascular plants are estimated to be polyploids, the potential for high rates of speciation in small areas probably continues to be high among these organisms. In contrast, speciation by polyploidy is rare among animals. Evidence suggests that most speciation events among animals depend on separation of a formerly continuous geographic range, either by imposition of a barrier to gene flow within the existing range or colonization of a new area by dispersing individuals. Subsequent evolution of differences sufficient to generate reproductive barriers should the populations again become sympatric may require thousands of years.

The current loss of species richness among Earth's existing biota is believed to be driven primarily by a striking increase in extinction rates. Rates of species formation are probably also declining but at a modest rate. For larger animals, current range contractions are probably reducing opportunities for subpopulations to survive long enough to lead to new species.

Increases in extinction rates have stimulated research to determine their causes, because if we wish to maintain Earth's biodiversity and preserve speciation opportunities, our primary task is to find ways to reduce the current high extinction rates. Extinctions are caused by many different agents and combinations of them, but the following few factors are believed currently to be the primary causes.

Habitat Loss and Fragmentation

Conversion of ecosystems to agriculture, forest plantations, rangelands dominated by domestic livestock, and urban and suburban development is greatly reducing the overall extent of many ecosystem types, and the remaining pieces are increasingly small and isolated from one another. Abundant evidence shows that species composition, interactions among species, and climates in small patches differ from those in large patches, and movements of individuals among patches are reduced. The habitats of many species with small ranges are being completely obliterated by conversion to other habitat types in which they cannot survive. Habitat loss and fragmentation are especially pronounced today in tropical forests, but fragmentation is also serious in other terrestrial habitats, especially grasslands. It may be important in some coastal marine regions, as well.

Although many ecosystem types were historically distributed in large, contiguous blocks, many others, such as lakes, reefs, caves, and outcrops of

unusual rock types, are typically highly dispersed and fragmented. Thus, organisms that live in them presumably evolved adaptations to survive in and disperse among isolated habitat patches. Species that live in formerly unfragmented habitats, on the other hand, are unlikely to have life history traits that adapt them for survival in small habitat patches. Therefore, conservation attention is appropriately concentrated on those species, but much can be learned by comparing their life history traits with those of species that evolved in patchy habitats.

Overexploitation

Much research has been carried out to assess maximum sustainable exploitation rates of commercially important species and to determine how those rates are influenced by life history traits of species and patterns of environmental variability. However, for primarily political and economic reasons, sustainable yield rates are typically exceeded, with the result that, for example, more than half of Earth's commercial fisheries are currently overexploited. A major trend in modern human societies is the expansion of the number of species that are traded in markets. Especially notable is the explosion of markets for ornamental plants and animals as pets. In addition, many fishing methods capture species that are not commercially important—bycatch—and typically discard them. Some harvesting methods, like dynamiting coral reefs and dredging the ocean floor, destroy the environments of both targeted and associated species.

Exotic Species

Natural processes have always moved individuals of species across substantial environmental barriers. Indeed, the biotas of some environments, such as oceanic islands, have been assembled entirely by such natural long-distance dispersal, followed by in situ speciation. Today, however, Earth's terrestrial and marine biota is being scrambled by an unprecedented movement of individuals of thousands of species by human activity. The biotas of many areas are now dominated by introduced species, and exotics are significant fractions of the biotas in other areas. In addition, many exotic species have become highly invasive and now dominate ecosystems in the areas in which they have become established. Extinction of native species by exotics appears to be relatively rare on continents, but it is common on islands. Nonetheless, major reductions in populations of native species, which are common consequences of invasions of exotics on mainland areas, are of considerable conservation concern.

Pollution

The waste products of human activities are now major components of Earth's atmosphere, soils, fresh waters, and oceans. Some of these materials are highly toxic substances that directly affect the health of organisms. Others are nutrients that cause undesirable effects at unnaturally high concentrations. Nutrient enrichment is especially important in fresh waters and coastal marine areas, but it is also significant in some terrestrial environments, especially those that are naturally nutrient poor. Some substances emitted to the atmosphere are neither nutrients or toxicants, but their increased concentrations result in alterations of the quantity and chemistry of precipitation.

Climate Change

Climates are never constant, and organisms have evolved traits that enable them to adjust to the range of variability that has characterized their environments. However, when climate variability exceeds levels to which organisms are adapted, many species may be unable to maintain viable populations. Considerable evidence exists to suggest that current human activities are perturbing Earth's atmosphere sufficiently to alter the current climate; the forcing factors, particularly greenhouse gases, especially carbon dioxide from burning fossil fuels, continue to increase. Therefore, increased climatic changes are anticipated. Even in the absence of direct anthropogenic effects, climatologists expect future climate variability to exceed that which has characterized the past few centuries. Increasing evidence suggests that extreme events may play powerful roles in determining changes in distribution and abundance of species, suggesting even greater needs for understanding the interaction between climate and biodiversity.

Targets of Conservation Activities—Problem of Baselines

Conservation practitioners work to achieve a variety of goals. They may seek to restore populations of an endangered species or to reintroduce a species into parts of its range from which it has been exterminated. They may attempt to remove an exotic species from a community that it is invading. They may try to reestablish a complex ecological community in an area from which it has been eliminated. They may wish to restore the primary productivity of an area or to reduce rates of soil erosion.

What all of these activities have in common is an attempt to reestablish some ecological state and functioning believed to have characterized a site at some time in the past. To do that, conservationists must make two key decisions. First, they must decide which time in the past should serve as the refer-

ence period. Second, they must assess the probable ecological conditions that existed in the area at that time. Neither of these decisions can be made using only scientific criteria. For example, in the United States, should we attempt to recreate ecological conditions as they were when humans first arrived from Asia? When Europeans first colonized North America? When chestnut blight first invaded eastern deciduous forests? When zebra mussels first invaded the Great Lakes? No unambiguous criteria exist for making these decisions. Value judgments may figure prominently and appropriately in deciding on reference periods.

Once a target period has been chosen, a practitioner must assess the probable ecological conditions that existed at that time. Sometimes paleontological or historical data are available to inform those guesses, but such data are always incomplete. The composition of the ecological community prior to the establishment of an exotic invader may be known only within wide limits. Even if the general composition of the former ecological community can be determined fairly precisely, should the goal be to recreate that composition as accurately as possible? Or should the goal be to recreate a community with a physical structure similar to the previous one? Or should a comparable level of biological productivity be sought? Again, multiple goals are possible, and it is not easy to determine which ones are most appropriate for a given situation. Some of the research priorities identified in the chapters to follow deal with methods designed to help make decisions about appropriate baselines, but no advances in conservation biology research will eliminate the need to make subjective judgments about baselines.

Major Themes

In the following eleven chapters, the status of knowledge in an array of fields is summarized, and critical gaps in knowledge that are currently impeding conservation practice in the field are described. For each topic a small number of high-priority research topics are identified. As the White Oak workshop unfolded, a small number of overarching research themes emerged:

- *Find ways to better use satellite imagery and aerial photographs to identify ecological systems and habitats and, if possible, the status of biodiversity within them.* Vast quantities of data are now being gathered by satellites orbiting Earth. For the most part, those data are being used to identify broad categories of land cover (agricultural lands, forests, urban and suburban areas) or to assess primary productivity. The potential of those data to serve as sources of information on habitat quality and species composition has scarcely been explored, especially for the marine environment.

- *Perform research to improve our understanding of the significance of alterations to the structure of food and interaction webs.* Local extinctions (extirpations) of native species, invasions of exotic species, and major changes in the relative abundances of species are likely to precipitate direct and indirect changes in ecological structure and processes, not to mention effects on the capacity of the system to provide goods and services for the human economy. The effective loss of highly interactive species is likely to initiate trophic cascades leading to the loss of species diversity.
- *Perform research to inform the design, development, and maintenance of marine protected areas.* Despite their potentially great importance, relatively little attention has been given to marine reserves, which account for less than 0.25 percent of the oceans. The current rate of alterations of coastal marine environments, especially coral reefs, gives special urgency to this concern.
- *Investigate the large-scale community and ecosystem impacts of eutrophication in marine and fresh waters.* Lakes, streams, rivers, and the oceans are the ultimate repositories of materials introduced into ecosystems. Yet little is currently known about where and how these materials enter aquatic environments, how they interact with the biotic and abiotic components of the ecosystems, what harmful consequences might occur, and what remedial actions should be devised.
- *Perform research to enable us to better predict which exotic species are likely to become invasive and what their effects will be.* In practice it is impossible to completely stop the importation of potentially troublesome exotic species, but significant improvements are possible, including restrictions on importing potentially invasive species and disease vectors. We need to become more adept, however, at identifying potentially harmful species and predicting their public health and ecological hazards.

Organization of the Book

The subsequent eleven chapters in this book are based on the discussion papers written prior to the White Oak workshop by the invited senior authors. They have been modified as a result of contributions by the designated respondents and other workshop participants, and converted to a general format. Each chapter assesses the current state of knowledge about the issue and identifies the gaps in knowledge that most strongly impede the ability of conservation practitioners to carry out their work. These two sections serve to motivate the research priorities that are proposed in the final

section of each chapter and highlighted in a box at the end of each chapter. A final synthesis chapter describes some of the changes that have occurred in the world and the field of conservation biology in the last twenty years and places research priorities in a broad political context.

LITERATURE CITED

Soulé, M. E., and J. Terborgh. 1999. *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Washington, D.C.: Island Press.

ASSESSMENT AND MANAGEMENT OF SPECIES AT RISK

Georgina M. Mace, Jonathan E. M. Baillie,
Steven R. Beissinger, and Kent H. Redford

A MASSIVE HUMAN POPULATION, DISTRIBUTED ACROSS MOST AREAS of the Earth's land surface, now competes directly and indirectly with other species for natural resources. As a result of human activities many species have gone extinct, others are restricted to tiny islands of remaining habitat, and still others are committed to extinction in the near future.

For still larger numbers, the future looks extremely uncertain. Recent assessments of the global conservation status of species (IUCN 1996; Oldfield et al. 1998) suggest that more than 10 percent of birds and around 20 percent of mammals and amphibians are now threatened with extinction (table 2.1). Comprehensive assessments of all native U.S. species by The Nature Conservancy show that over 60 percent of molluscs and crayfish, 40 percent of freshwater fishes and amphibians, and 50 percent of freshwater invertebrates are at risk. Extinction risk also is demonstrably nonrandom; species within some phylogenetic clades tend to have higher or lower levels of extinction risk than across taxa as a whole, thereby increasing the loss of evolutionary diversity from species extinctions (Russell et al. 1998; Purvis, Agapow, et al. 2000). Extinctions are also nonrandom with respect to the ecological roles that species play such that loss of certain species will have a disproportionate impact on ecosystems (Jernvall and Wright 1998), as described in chapter 3.

TABLE 2.1. Summary Results of the Application of IUCN Criteria to Various Higher Taxonomic Groupings

Taxon	Approximate number of species assessed	Percent threatened of those assessed	Percent data deficient of total assessed
Mammals	4763 (100%)	23	5
Birds	9946 (100%)	11	1
Reptiles	1480 (20%)	17	5
Amphibians	600 (12%)	21	7
Molluscs	>3000 (4%)	31	18
Trees	10,091 (0.1%)	59	4

Note: The approximate number of species assessed is estimated from IUCN (1996) and Oldfield et al. (1998). The figure in parentheses indicates the proportion assessed of the total species diversity in the group. Since assessors may focus on the most threatened species, and on those that are well known, the threat and data deficiency rates may become more unrepresentative as the proportion of species assessed decreases.

The situation is more serious still for some taxonomic groups in especially vulnerable habitats. Certain dramatic evolutionary radiations have been almost completely eliminated. For example, until the mid-1980s over 120 land snail species of the snail family Partulidae were distributed across the islands of Polynesia; almost all are now either critically endangered or extinct as a result of the introduction of a predatory snail (Mace et al. 1998). The introduction of the Nile perch (*Lates niloticus*) to Lake Victoria in East Africa has now led to the extinction of up to two hundred species of haplochromine cichlid fishes that once formed a unique "species flock" with extraordinary levels of morphological, ecological, and behavioral specializations. These examples illustrate the intensity and potential of the current extinction spasm.

From the perspective of a research agenda, we need to analyze the causes and understand the processes that ultimately lead to species extinction, and thus identify methods and approaches to mitigate the problem. In this chapter we review some key issues for the assessment and management of species at risk.

Habitat Loss, Overexploitation, and Introduced Species

Species have always gone extinct. The fossil record bears testament to the extinctions of both species and entire evolutionary radiations, and extant species probably represent only about 2–4 percent of all species that have

ever lived (May et al. 1995). The fragmentary nature of the fossil record makes direct comparison of ancient extinctions with modern extinction problematic (Jablonski 1995). Most paleontological data come from marine invertebrates, usually of abundant and widespread taxa, while modern extinctions have mostly been cataloged for terrestrial vertebrates, many of which were relatively rare and narrowly distributed. Some authors have suggested that, based on the average persistence time of species in the fossil record of between 0.5 and 10 million years, the current extinction rate may be from one hundred to one thousand, and perhaps ten thousand, times higher than background extinction rates (May et al. 1995; Pimm et al. 1995).

Extinction rates have varied throughout the fossil record, with noticeable peaks during periods of mass extinction (Jablonski 1991; Benton 1995; May et al. 1995). The rates that we expect over the coming centuries may begin to approach the most severe periods of extinction in the earth's history (Jablonski 1995). Unlike the mass extinctions of the past, however, the driving processes are not attributable to abiotic geological changes or extraterrestrial impacts. Instead, the direct and indirect causes are almost entirely due to human activities. Our analysis of the nature of extinctions must therefore start with a consideration of these ultimate driving processes.

The major processes leading to extinction are anthropogenic and result from habitat loss, overexploitation, introduced species, and the interactions among these (Diamond 1989). These processes may be regarded as the extrinsic drivers, the ultimate causes of extinction as described by Simberloff (1986), or the agents behind the "declining population paradigm" described by Caughley (1994).

Habitat loss is probably the most common problem, especially for continental species (WCMC 1992; Mace and Balmford 2000). Human population growth and development lead to the appropriation of extensive areas of land for settlement, agriculture, and resource extraction, and the infrastructure to support these activities causes further loss and fragmentation. Habitat loss implies not just clearance but also all kinds of degradation and fragmentation that limit the potential for wild species to persist. Over large continental areas—for example, in northwest Europe and eastern North America—natural habitats are now reduced to a tiny proportion of their historical extent, and many of the land areas set aside for wildlife are degraded and left for conservation management largely because they are unsuitable for development. As the patches of remaining habitat become smaller and more isolated, the species living within them are more likely to go extinct and individuals from neighboring patches are unable to immigrate to repopulate the patch. In eastern North America, species extinctions have been recorded at a rate consistent with simple models concerning the effects of habitat loss (Pimm and

Askins 1995). Other regions, such as the species-rich eastern coastal forests of Brazil, which have endured relatively recent yet extensive clearance, have so far suffered few recorded extinctions. However, large numbers of species restricted to small remaining patches of forest, though not extinct, appear to have very bleak prospects (Brooks and Balmford 1996). Following their isolation in habitat remnants, species may persist for some time before finally succumbing (Brooks et al. 1999; Cowlshaw 1999), perhaps giving us too optimistic a view of the eventual impact of our current activities.

Overexploitation can take a variety of forms, from large-scale commercial extraction of fishes and forests to local, subsistence hunting. There are often limited controls to the access to wildlife resources, providing little incentive to manage the resource sustainably (Hardin 1999). This creates competition that is hard to regulate efficiently, even when there are technical and financial resources to do so (Ludwig et al. 1993). Despite extensive research into methods for sustainably harvesting natural populations, there are still many difficulties in estimating key parameters and implementing and enforcing management plans (Ludwig et al. 1993; Lande et al. 1994). As a result, for example, although the total commercial catches of marine fishes have been relatively constant over the last few decades, data from the Food and Agriculture Organization of the UN (FAO) show a shift in catch records from long-lived, high-trophic-level, piscivorous bottom fish toward short-lived, low-trophic-level invertebrates and planktivorous pelagic fish. These trends signal unsustainable exploitation of marine resources and seem likely to have both direct and indirect impacts on oceanic food webs and communities (Pauly et al. 1998). Indeed, several commercially exploited fish species now show continuing declines in abundance despite international agreements to control their harvest rates (Cook et al. 1997; Myers et al. 1997; Matsuda et al. 1998). Large, long-lived, and slowly reproducing species appear to be the most vulnerable to declines from commercial fishing (Jennings et al. 1998), and one such species, the barndoor skate (*Raja laevis*), now appears to be close to extinction (Casey and Myers 1998).

At more local scales, overharvesting for food, fuelwood, pets, ornaments, and trophies continues to threaten many species. Although international agreements limit the trade in wild species among countries, there are difficulties in controlling exploitation within countries, especially where the wildlife products are of high commercial value (e.g., elephants [Milner-Gulland and Beddington 1993]). Many wild species are also unsustainably harvested in tropical forests as a source of protein (e.g., neotropical vertebrates [Alvard 1997]). Hunting for bushmeat is a serious threat to many wildlife species because the characteristics that make species attractive as a source of protein, such as large body size, also make the species especially vulnerable to overhunting (Robinson and Redford 1991).

Introductions and translocations of species to areas outside their natural ranges are now, and have been, a major driver of anthropogenic extinctions. Many species, especially in areas that have been settled by people from distant lands, have already been driven extinct by introduced species. Pimm et al. (1994) estimate that the Polynesians wiped out five hundred to one thousand bird species in their early explorations across the Pacific, and introductions continue to pose a serious threat to island species (WCMC 1992). Similarly, the Australian mammal fauna has suffered directly and indirectly from introduced species, especially European native species brought by early settlers (Burbidge and McKenzie 1989). The highly diverse endemic plant radiation of the Cape Floristic province of South Africa is threatened by both invasive species and land-use changes. Successful invasive species generally tend to be short lived, with high intrinsic rates of increase, i.e., early successional species. Although they outcompete native species in the short term, over the long term the ability of some invasive species to persist may be limited. In contrast, the species that are most susceptible to the effects of introduced species are those that inhabit isolated regions and occupy habitats that have been heavily modified by anthropogenic influences (Godfray and Crawley 1998), where they may suffer population declines and extinction from competition, predation, or hybridization.

Consequences of Extrinsic, Human-Caused Perturbations

A species' vulnerability to extrinsic threats is often influenced by its ecology, life history, physiology, or distribution. Intrinsic characteristics of extinction-prone species have been more thoroughly investigated by research biologists than have the effects of the external drivers and the interactions between the two (Caughley 1994), leading to some debate about the relative importance of each. However, it is clear that both factors should be considered if we are to improve the reliability of predictions about extinction risk (Hedrick et al. 1996; Beissinger and Westphal 1998).

Several kinds of evidence provide information about the most vulnerable species. First, empirical studies have identified intrinsic characteristics of extinction-prone species. Rates of local extinction have been shown to be higher for species that have restricted ranges or occupy a small number of sites (Hanski 1982; Simberloff and Gotelli 1984; Thomas and Mallorie 1985; Happel et al. 1987; Gaston 1994; Gaston and Blackburn 1996; Gaston and Chown 1999); are local endemics (Terborgh and Winter 1980; Cowling and Bond 1991); or have low abundances, high temporal population variability, and poor dispersal (Karr 1982; Diamond 1984; Pimm et al. 1988; Newmark 1991; Gaston 1994). These studies are all open to the criticism that they may be investigating only correlates of extinction-prone characteristics, since body size, dispersal ability, range size, population variability, and local population

density are all interrelated (McArdle et al. 1990; Pimm 1992; Gaston 1994; Gaston and Blackburn 1996). In studies where interrelationships among life history traits and the geographical sampling can be controlled, extinction risk has been shown to be higher for species with low population density, small range size, and habitat and diet specializations (Foufopoulos and Ives 1999; Purvis, Gittleman et al. 2000). The response of a species to a threat is complicated and depends on its life history, the local environmental conditions, and the specific perturbation. For example, the stability of fluctuating populations is reduced by exploitation (Beddington and May 1977); the response of primates to logging is a function of their home-range size and the latitude at which they live (a correlate of habitat variability) (Harcourt 1997); and extinction of carnivores within reserves is higher for those with large home ranges (Woodroffe and Ginsberg 1998).

Second, ecological and life history theory provides some useful insights. It can be shown that small populations are more extinction prone because of their susceptibility to demographic stochasticity (Richter-Dyn and Goel 1972; Goodman 1987); the increased expression of recessive deleterious alleles under inbreeding (Soulé 1980; Soulé and Mills 1998); the change in quantitative characters that allow adaptation; and the accumulation of mildly deleterious mutations (Hedrick and Miller 1992; Frankham 1995a).

Lande (1998) has reviewed these various processes in terms of the minimum viable population sizes that they imply. This has shown that demographic stochasticity is unlikely to be important for any population that has more than one hundred individuals, but random environmental variation or catastrophes are important for populations of all sizes, and they become more significant as environmental variability becomes large in relation to the population growth rate (Lande 1993).

In terms of genetic effects, deleterious recessive alleles become more likely to be expressed when populations are reduced in number. The resulting inbreeding depression may increase short-term effective population size (N_{es}) up to 50–100 (Mills and Smouse 1994; Allendorf and Ryman in press), translating to effects on actual population size in the range of 200–500 individuals (Soulé et al. 1986; Mace and Lande 1991; Frankham 1995b). To preserve quantitative trait variation, larger populations are needed. One estimate is that to maintain high levels (more than 90 percent) over thousands of years will require minimum effective population sizes of at least 5,000, and to prevent the accumulation of mildly deleterious mutations over tens of thousands of years will require minimum effective population sizes of around 10,000 to 100,000. Because of difficulties in estimating key parameter values for these calculations (Franklin and Frankham 1998; Lynch and Lande 1998; Waples in press), the critical population sizes from these theoretical studies are best interpreted as guides to the relative importance of dif-

ferent characteristics rather than as real thresholds for management (Lande 1998). Moreover, this approach is deficient because it lacks a treatment of the feedbacks between genetics and demography (Soulé and Mills 1998).

Our analysis of the extrinsic and intrinsic factors associated with increased extinction risk has covered much of the field of ecology and evolutionary biology. In order to identify key questions, in the following sections we analyze issues that are of practical significance for conservation practitioners.

Critical Gaps in Knowledge

In discussing the critical gaps in our knowledge about how to protect species at risk, we will examine six major areas. Research priorities for these six areas are given in box 2.1. The research areas are:

- Identifying patterns of species at risk
- Investigating the dynamics of threatening processes
- Investigating the dynamics of population persistence in a changing world
- Assessing the effectiveness of different management strategies
- Incorporating the human dimension in conservation
- Implementing adaptive management and monitoring

Each of these subjects is discussed below, and pertinent research questions are identified. First we discuss research questions, then move on to management actions.

Research Questions

Identifying Patterns of Species at Risk

The first set of research questions requires an analysis of patterns—a simple accounting of where the most species are located and what their relative risks of extinction, endemism, and diversity are. Along with patterns of biodiversity it is important to document the distribution and intensity of dominant processes of threat throughout different regions of the world. The above issues are particularly relevant to the design of networks of protected areas (Soulé and Terborgh 1999). This approach has been widely explored and used for planning at both global and regional levels. Through such studies, high-priority areas, habitats, and ecosystems have been identified and targeted for action (Myers 1988, 1990; Pressey et al. 1993; Beissinger et al. 1996; Williams 1998). Species are not distributed evenly over the earth's surface, and neither are the centers of richness, endemism, or threat particularly well correlated across taxa (WCMC 2000), especially in certain regions, such as the United Kingdom and South Africa (Prendergast et al. 1993; van Jaarsveld et al. 1998). In other areas, there are higher congruence patterns of species' complemen-

tarity among sites, such as forest patches in Uganda (Howard et al. 1998). In general, however, the concordance among diversity, endemism, and threat—three different measures of the conservation importance of an area—also varies with scale and location (Balmford and Long 1995; Kershaw et al. 1995) and presents some difficult choices for those setting conservation priorities (Margules et al. 1988; Pressey et al. 1996).

Investigating the Dynamics of Threatening Processes

Analyzing patterns provides only a partial solution. The viability of populations and species ultimately depends upon population and evolutionary dynamics. Within any particular area, species will not share similar future prospects. Those that are highly adaptable (genetically, behaviorally, or both), have good dispersal abilities, or belong to populations whose prospects are more favorable will be expected to have enhanced viabilities. Therefore, we consider the dynamics of threatening processes and their likely impact upon affected species.

Investigating the Dynamics of Population Persistence in a Changing World

A simple consideration of threatening processes reveals that these change in nature and intensity over both time and space—sometimes at alarming rates. This is one reason analyses of patterns do not provide a sufficient basis for management (Smith et al. 1993; Balmford et al. 1998). Our third set of research topics considers studies on how species at risk can cope with dynamic change.

Currently, dynamic changes are accentuated as a result of the rapid human population expansion. Numbers are still increasing rapidly, although at different rates in different areas of the world (Cohen 1995). Globally, human numbers are expected to double over the next sixty years (McNeely et al. 1995). While some regions, such as Europe and North America, are expected to meet their resource needs without further land conversion for agriculture, many other areas are still undergoing rapid development alongside high population growth. Food requirements may double in Central and South America and Asia, and perhaps increase fivefold in Africa (WCMC 2000). Land-use changes will therefore proceed inexorably in some areas of high biodiversity. This demand, and its likely impact on wild species, needs to be understood and managed if conservation activities are to be successful. Even in more stable areas of the world, changing patterns of work and leisure are leading to migrations from urban to rural areas, with significant consequences for land-use planning. Habitat loss and fragmentation will continue but at different rates and in different ways than in the past.

One of the difficulties with the dynamic nature of land changes is that past trends are often not a reliable predictor of the future. Human activities also present a new challenge in the form of global climate change. Current predictions about changes in average temperatures suggest that the impacts will vary regionally and across habitats. There may be profound influences on marine ecosystems, which could experience an increased frequency and intensity of oceanic perturbations with consequences for many marine fish and corals. Global patterns of seawater circulation are expected to alter as a result of increased surface temperatures, which may have consequences for sea levels and for climate in both island and continental areas. Some parts of the land surface, especially temperate and arctic zones, are expected to face large temperature changes, and there is already evidence that European bird and butterfly species ranges are shifting to higher latitudes and animals are altering egg-laying dates in response to current warming trends (Crick and Sparks 1999; Hill et al. 1999; Thomas and Lennon 1999). Under systematic warming, species persistence will depend on a different set of traits than those that offer high fitness in more stable habitats. All this underlines the importance of studying and understanding the spatial, temporal, and adaptational characteristics of species. For example, a study of a forest savannah in Cameroon indicated that, although ecotones have generally been regarded as unimportant areas, natural selection operating on birds in the ecotone may be important for generating evolutionary novelties (Smith et al. 1993).

Management Actions

The final three groups of research priorities discussed below focus on ways to use knowledge gained from research in the development, implementation, and assessment of management activities. Many conservation practices have been tried in the past, some with much more success than others. Unfortunately these experiences are often poorly documented, and knowledge disappears with the people who were responsible for it. A more systematic approach to analyzing and synthesizing alternative approaches is needed.

Assessing the Effectiveness of Different Management Strategies

In this section, we focus on the more biological aspects of management at both the population and ecosystem levels. Fundamental principles from population biology were first developed a couple of decades ago (Soulé 1987). A variety of ever more sophisticated techniques for population management now incorporate environmental and human processes in various forms of population viability analysis (PVA) (Boyce 1992; Burgman et al. 1993). While some empirical evidence suggests that these models are reliable predictors of

BOX 2.1. Research and Management Priorities

Research Priorities

Identifying Patterns of Species at Risk

1. Which regions, habitats, taxa, and species are most threatened or soon will be?
2. What are the major processes threatening biodiversity, and where are they currently focused? How do these processes change over time and space?
3. What are the current population trends of species in different locations? Can a valid index of community or ecosystem health based on many species and processes be developed?
4. What do studies of recent and historical correlates among extinction rates, anthropogenic processes, and biological features of species indicate about simple measures that can be used to direct conservation activities? What is the evidence that extinction filters, selective processes of past extinction, have already stripped out vulnerable taxa and communities? Can such knowledge ensure that conservation efforts be directed toward systems that have been less exposed to threats and are therefore more vulnerable to them?
5. Can habitat loss be used as a surrogate to estimate rates of extinction? If so, how will factors such as species richness, habitat type, and latitude influence the calibration?
6. Are indicator, keystone, or flagship species effective conservation monitoring tools, and if so, which species or complex of species best represent the status of a larger system?

Investigating the Dynamics of Threatening Processes

1. How do aspects of species ecology, behavior, genetics, phylogenetic status, and life history affect a species' ability to acclimate and persist in response to the following: habitat loss, fragmentation, and modification; introduction of exotic species; exploitation for sustainable use; introduction of new diseases; and other anthropogenic threats and disturbances?
2. To what degree do extinction lag effects inhibit the identification of species that are at great risk of extinction?
3. What determines when extinction is the endpoint of a decline? Are species that have successfully adapted to the human landscape simply behaviorally preadapted, or are some species better able than others to adapt through learning?
4. What are the best methods for diagnosing population decline? Experimental and comparative methods for diagnosing causes of population decline need to be developed and tested.
5. How important are cumulative threats to the persistence of species? What kinds of interactions among threats are the most severe?
6. What combinations of spatial patterns and biological or physical factors (e.g., nutrient balance, rarity, and abundance) are the most efficient and useful indicators of changing population and ecosystem processes?

7. Can new approaches, such as molecular genetic methods, be used to obtain rapid insight into a species' population dynamics when long-term data are lacking?

Investigating the Dynamics of Population Persistence in a Changing World

1. What determines variation in the resilience of communities or ecosystems? How is it affected by recent isolation, species richness, trophic-level distribution, alien species, humidity, latitude, niche occupation, life history, functional redundancy, and keystone species?
2. How do population dynamics and persistence vary in relation to life history attributes, population structure, environments, and phylogeny? How are habitat types and ecological factors such as ecotones, marginal habitats, niche availability, or the edge of a species range associated with persistence?
3. How much and at what spatial scales does demography vary within a metapopulation and across landscapes? Can sources and sinks be identified given their true definitions? How often do different types of metapopulations and source-sink dynamics occur in nature?
4. What is the relative importance of demographic and environmental stochasticity in affecting extinction compared to biological features of species and anthropogenic factors?
5. To what degree and under what conditions does genetic variation influence demography and persistence? How does inbreeding in small populations affect persistence? How does outbreeding depression affect persistence in admixed populations? What is the relative importance of gene flow versus local adaptation for population persistence? How does genetic architecture of a trait influence its potential for adaptive change?

Management Actions and Priorities

Assess the Effectiveness of Different Management and Implementation Strategies

1. How can the models used in decision making be improved? What is the appropriate context for use of population viability analysis, decision analysis, and other analytical techniques that are intended to guide managers?
2. How should reserves be designed to reflect dynamic landscapes? How large need reserves be so that difficult and expensive management regimes are not required to replace former ecological processes?
3. What conservation strategies maximize both species and community conservation and fulfill specific human needs? When is it best to focus conservation resources on strictly protected areas versus integrated land-use areas? What are the biological and economic costs and benefits of strategies that focus on prevention versus cure? What are the biological and economic costs and benefits of focusing on reversible threats and species that can be saved while rejecting difficult cases, compared to focusing on saving the most threatened first (i.e., triage approaches)?

(continues)

BOX 2.1 (*Continued*)

4. How useful are rules of thumb for conservation planning and population viability assessment? Can they be tested using a combination of modeling techniques and empirical studies?
5. What are the biological and economic costs and benefits of captive breeding, reintroductions, and translocations? How frequently does adaptation to captive propagation prevent successful reintroductions of plants and animals? How can the process of domestication and adaptation be reversed in captive animal and plant populations?
6. What incentives can be used to encourage conservation organizations to share information and pool resources for common projects?

Incorporate the Human Dimension in Conservation

1. What are the most useful approaches to involve local communities in conservation projects? What can we learn from projects that have and have not been successful in accomplishing this? How can we ensure that local support for conservation projects is sustainable over long periods of time?
2. What organizational models lead to improved implementation, coordination, and scientific direction of endangered species recovery programs?
3. How can we plan protected areas and other management units so that they require minimal long-term management, or political and social controls?

Implement Adaptive Management and Monitoring

1. How should managers monitor, assess, and disseminate results of conservation projects? What can be learned from implementation of management recommendations that should feed back into the research agendas and future planning options?
2. What aspects of structure, power, and authority in governmental and non-governmental organizations enhance or decrease the implementation of adaptive management approaches in decision making?
3. How can management interventions be structured to test theory and collect data to learn from crises?
4. Where should assessment and monitoring be targeted—individual organisms; populations; subspecific units and species; or assemblages of species that are grouped by habitat, ecoregion, phylogeny, or functional criteria? What are the economic and biological consequences of adopting any one of these for a specific instance?

future population trends (Brpok et al. 2000), it is unclear how robust they are as management tools when vital rates are well known (Fieberg and Ellner 2000), let alone under uncertainty and catastrophic change (Mangel and Tier 1994; Ludwig 1996); and it is also unclear how best to incorporate many different variables and their interactions into such models (Beissinger and Westphal 1998).

Incorporating the Human Dimension in Conservation

Culture and place affect the choice of conservation tactics. For example, the United States has strong species-based legislation that provides protection for the habitats of listed species in their native areas, whereas in Australia and New Zealand translocations, introductions, and reintroductions have been extensively used for some highly endangered species (Serena and Williams 1994). The role of captive breeding has been widely debated (Hutchins et al. 1995; Balmford et al. 1996; Snyder et al. 1996). The practitioners of many regions focus conservation efforts on the design, implementation, and management of protected areas and reserves (Soulé and Terborgh 1999). In a rapidly changing environment and landscape, it is increasingly difficult to design protected areas that will be efficient in the future. Placing reserves at natural landscape scales with edges at natural boundaries should be efficient (Peres and Terborgh 1995), but the designs and configuration of reserve areas may need to be altered to cope with systematic environmental changes, especially climate change.

We recognize both the challenges and benefits associated with local human communities whose immediate needs and aspirations may conflict with those of biodiversity conservation. While some apparent conflicts are illusory, in other cases strategies and approaches can be taken that will be more effective at achieving multiple short- and long-term goals. It is in this area in particular that conservation biologists must move into more interdisciplinary scientific communities and work with economists, sociologists, land planners, and human demographers to achieve effective results.

Implementing Adaptive Management and Monitoring

A long-term approach to management that includes both monitoring, analysis of actions, and adaptive management is important. Once management plans are in place, the predetermined goals and objectives should be evaluated regularly; if the actions are not proceeding according to plan, then the reasons need to be identified and alterations made (Margoluis and Salafsky 1998). For effective adaptive management, a great deal of planning must be undertaken at the start, with agreement among various stakeholders about what the indicators of altered management might be. Biologists should play

an active role in such planning to ensure that the biological principles at the heart of any management plan are not compromised as implementation proceeds.

LITERATURE CITED

- Alvard, M., J. Robinson, K. Redford, and H. Kaplan. 1997. The sustainability of subsistence hunting in the neotropics. *Conservation Biology* 11:977–982.
- Balmford, A., and A. Long. 1995. Across-country analyses of biodiversity congruence and current conservation effort in the tropics. *Conservation Biology* 9:1539–1547.
- Balmford, A., G. Mace, and J. Ginsberg. 1998. Challenges to conservation in a changing world. In G. M. Mace, A. Balmford, and J. Ginsberg (eds.), *Conservation in a Changing World*, pp. 1–28. Cambridge: Cambridge University Press.
- Balmford, A., G. M. Mace, and N. Leader-Williams. 1996. Redesigning the ark: Setting priorities for captive breeding. *Conservation Biology* 10:719–727.
- Beddington, J. R., and R. M. May. 1977. Harvesting populations in a randomly fluctuating environment. *Science* 197:463–465.
- Beissinger, S. R., E. C. Steadman, T. Wohlgemant, G. Blate, and S. Zack. 1996. Null models for assessing ecosystem conservation priorities: Threatened birds as titers of threatened ecosystems in South America. *Conservation Biology* 10:1343–1352.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- Benton, M. J. 1995. Diversification and extinction in the history of life. *Science* 268:52–58.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481–506.
- Brook, B. W., J. J. O'Gady, A. P. Chapman, M. A. Burgman, H. R. Akcakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385–387.
- Brooks, T., and A. Balmford. 1996. Atlantic forest extinctions. *Nature* 380:115.
- Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* 13:1140–1150.
- Burbidge, A. A., and N. L. McKenzie. 1989. Patterns in the modern decline of western Australia's native fauna: Causes and conservation implications. *Biological Conservation* 50:143–198.
- Burgman, M. A., S. Ferson, and H. R. Akcakaya, eds. 1993. *Risk Assessment in Conservation Biology*. London: Chapman & Hall.
- Casey, J. M., and R. A. Myers. 1998. Near extinction of a large, widely distributed fish. *Science* 281:690–692.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215–244.
- Cohen, J. E. 1995. *How Many People Can the Earth Support?* New York: W.W. Norton.

- Cook, R. M., A. Sinclair, and G. Stefansson. 1997. Potential collapse of North Sea cod stocks. *Nature* 385:521–522.
- Cowling, R. M., and W. J. Bond. 1991. How small can reserves be—An empirical approach in Cape Fynbos, South Africa. *Biological Conservation* 58:243–256.
- Cowlishaw, G. 1999. Predicting the pattern of decline of African primate diversity: An extinction debt from historical deforestation. *Conservation Biology* 13:1183–1193.
- Crick, H. Q. P., and T. H. Sparks. 1999. Climate change related to egg-laying trends. *Nature* 399.
- Diamond, J. M. 1984. “Normal” extinctions of isolated populations. In M. H. Nitecki (ed.), *Extinctions*, pp. 191–246. Chicago: University of Chicago Press.
- Diamond, J. M. 1989. The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society, London, Series B* 325:469–477.
- Fieberg, J., and S. P. Ellner. 2000. When it is meaningful to estimate an extinction probability? *Ecology* 81:2040–2047.
- Foufopoulos, J., and A. R. Ives. 1999. Reptile extinctions on land-bridge islands: Life-history attributes and vulnerability to extinction. *American Naturalist* 153: 1–25.
- Frankham, R. 1995a. Conservation genetics. *Annual Review of Genetics* 29:305–327.
- Frankham, R. 1995b. Effective population-size adult population-size ratios in wildlife—A review. *Genetical Research* 66:95–107.
- Franklin, I. R., and R. Frankham. 1998. How large must populations be to retain evolutionary potential? *Animal Conservation* 1:69–70.
- Gaston, K. J. 1994. *Rarity*. London: Chapman and Hall.
- Gaston, K. J., and T. M. Blackburn. 1996. Global scale macroecology: Interactions between population size, geographic range size and body size in the Anseriformes. *Journal of Animal Ecology* 65:701–714.
- Gaston, K. J., and S. L. Chown. 1999. Geographic range size and speciation. In A. E. Magurran and R. M. May (eds.), *Evolution of Biological Diversity*, pp. 236–259. Oxford: Oxford University Press.
- Godfray, H. C. J., and M. J. Crawley. 1998. Introductions. In W. J. Sutherland (ed.), *Conservation Science and Action*, pp. 39–65. Oxford: Blackwells.
- Goodman, D. 1987. The demography of chance extinction. In M. E. Soulé (ed.), *Viable Populations for Conservation*, pp. 11–34. Cambridge: Cambridge University Press.
- Hanski, I. 1982. Dynamics of regional distribution: The core and satellite species hypothesis. *Oikos* 38:210–221.
- Happel, R. E., J. F. Noss, and C. W. Marsh. 1987. Distribution abundance and endangerment of primates. In C. W. Marsh and R. A. Mittermeier (eds.), *Primate Conservation in the Tropical Rain Forest*, pp. 63–82. New York: Alan R. Liss.
- Harcourt, A. 1997. Ecological indicators of risk for primates as judged by species’ susceptibility to logging. In T. Caro (ed.), *Behavioural Ecology and Conservation Biology*, pp. 56–79. New York: Oxford University Press.
- Hardin, G. 1999. The tragedy of the commons revisited. *Environment* 41:5+.
- Hedrick, P. W., R. C. Lacy, F. W. Allendorf, and M. E. Soulé. 1996. Directions, in

- Conservation Biology* comments on Caughley. *Conservation Biology* 10:1312–1320.
- Hedrick, P. W., and P. S. Miller. 1992. Conservation genetics: Techniques and fundamentals. *Ecological Applications* 2:30–46.
- Hill, J. K., C. D. Thomas, and B. Huntley. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London, Series B* 266:1197–1206.
- Howard, P. C., P. Viskanec, T. R. B. Davenport, F. W. Kigenyi, M. Baltzer, C. J. Dickinson, J. S. Lwanga, R. A. Matthews, and A. Balmford. 1998. Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature* 394:472–475.
- Hutchins, M. K., K. Willis, and R. J. Wiese. 1995. Strategic collection planning: Theory and practice. *Zoo Biology* 14:5–25.
- IUCN. 1996. *The 1996 IUCN Red List of Threatened Animals*. Gland, Switzerland: IUCN.
- Jablonski, D. 1991. Extinctions: A palaeontological perspective. *Science* 253:754–757.
- Jablonski, D. 1995. Extinctions in the fossil record. In J. H. Lawton and R. M. May (eds.), *Extinction Rates*, pp. 389–391. Oxford: Oxford University Press.
- Jennings, S., J. Reynolds, and S. Mills. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London, Series B* 265:333–339.
- Jernvall, J., and P. C. Wright. 1998. Diversity components of impending primate extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 95:11279–11283.
- Karr, J. R. 1982. Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* 63:1975–1978.
- Kershaw, M., G. M. Mace, and P. H. Williams. 1995. Threatened status, rarity, and diversity as alternative selection measures for protected areas: A test using Afrotropical antelopes. *Conservation Biology* 9:324–334.
- Lande, R. C. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911–927.
- Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction. In G. M. Mace, A. Balmford, and J. R. Ginsberg (eds.), *Conservation in a Changing World*. Cambridge: Cambridge University Press.
- Lande, R., S. Engen, and B. E. Saether. 1994. Optimal harvesting, economic discounting and extinction risk in fluctuating populations. *Nature* 372:88–90.
- Ludwig, D. 1996. Uncertainty and the assessment of extinction probabilities. *Ecological Applications* 6:1067–1076.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation—Lessons from history. *Science* 260:17.
- Lynch, M., and R. Lande. 1998. The critical effective size for a genetically secure population. *Animal Conservation* 1:70–72.
- Mace, G. M., and A. Balmford. 2000. Patterns and processes in contemporary mammalian extinctions. In A. Entwistle and N. Dunstone (eds.), *Priorities for the Conservation of Mammalian Biodiversity*. Cambridge: Cambridge University Press.

- Mace, G. M., and R. Lande. 1991. Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5:148–157, Special Publication No. 2.
- Mace, G. M., P. Peace-Kelly, and D. Clarke. 1998. An integrated conservation programme for the tree snails of Polynesia (Partulidae): A review of captive and wild elements. *Journal of Conchology* (special publication) 2:89–96.
- Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75:607–614.
- Margoluis, R. A., and N. N. Salafsky. 1998. *Measures of Success*. Washington, D.C.: Island Press.
- Margules, C. R., A. O. Nicholls, and R. L. Pressey. 1988. Selecting networks of reserves to maximise biological diversity. *Biological Conservation* 43:63–76.
- Matsuda, H., Y. Takenaka, T. Yahara, and Y. Uozumi. 1998. Extinction risk assessment of declining wild populations: The case of the southern bluefin tuna. *Researches on Population Ecology* 40:271–278.
- May, R. M., J. H. Lawton, and N. E. Stork. 1995. Assessing extinction rates. In J. H. Lawton and R. M. May (eds.), *Extinction Rates*. Oxford: Oxford University Press.
- McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations: Patterns, problems and artefacts. *Journal of Animal Ecology* 59:439–454.
- McNeely, J. A., M. Gadgil, C. Leveque, C. Padoch, and K. Redford. 1995. Human influences on biodiversity. In V. H. Heywood (ed.), *Global Biodiversity Assessment*, pp. 510–519. Cambridge: Cambridge University Press.
- Mills, L. A., and P. E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. *American Scientist* 144:412–431.
- Milner-Gulland, E. J., and J. R. Beddington. 1993. The exploitation of elephants for the ivory trade—An historical perspective. *Proceedings of the Royal Society of London, Series B* 252:29–37.
- Myers, N. 1988. Threatened biotas: “hotspots” in tropical forests. *Environmentalist* 8:187–208.
- Myers, N. 1990. The biodiversity challenge: Expanded hotspots analysis. *Environmentalist* 10:243–256.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* 7:91–106.
- Newmark, W. D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. *Conservation Biology* 5:67–78.
- Oldfield, S., C. Lusty, and A. MacKinnon, eds. 1998. *The World List of Threatened Trees*. Cambridge: World Conservation Press.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. *Science* 279:860–863.
- Peres, C. A., and J. W. Terborgh. 1995. Amazonian nature reserves—An analysis of the defensibility status of existing conservation units and design criteria for the future. *Conservation Biology* 9:34–46.
- Pimm, S. L. 1992. *The Balance of Nature*. Chicago: University of Chicago Press.

- Pimm, S. L., and R. A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Science of the United States of America* 92:9343–9347.
- Pimm, S. L., H. L. Jones, and J. M. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757–785.
- Pimm, S. L., M. P. Moulton, and L. J. Justice. 1994. Bird extinctions in the central Pacific. *Philosophical Transactions of the Royal Society at London, Series B* 344: 27–33.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* 269:347–350.
- Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. C. Eversham, and D. W. Gibbons. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365:335–337.
- Pressey, R. L., C. J. Humphries, C. R. Margules, R. I. Vanewright, and P. H. Williams. 1993. Beyond opportunism—Key principles for systematic reserve selection. *Trends in Ecology & Evolution* 8:124–128.
- Pressey, R. L., H. P. Possingham, and C. R. Margules. 1996. Optimality in reserve selection algorithms: When does it matter and how much? *Biological Conservation* 76:259–267.
- Purvis, A., P.-M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288:328–330.
- Purvis, A., J. L. Gittleman, G. C. Cowlishaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society of London, Series B*. 267:1947–1952.
- Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonising species. *Theoretical Population Biology* 3:406–433.
- Robinson, J. G., and K. H. Redford. 1991. Sustainable harvest of neotropical forest mammals. In J. G. Robinson and K. H. Redford (eds.), *Neotropical Wildlife Use and Conservation*, pp. 415–429. Chicago: University of Chicago Press.
- Russell, G. J., T. M. Brooks, M. M. McKinney, and C. G. Anderson. 1998. Present and future taxonomic selectivity in bird and mammal extinctions. *Conservation Biology* 12:1365–1376.
- Serena, M., and G. A. Williams. 1994. Wildlife conservation and reintroduction: An Australian perspective. In M. Serena (ed.), *Reintroduction Biology of Australian and New Zealand Fauna*, pp. 247–252. Chipping Norton, New South Wales, Australia: Surrey Beatty and Sons.
- Simberloff, D. 1986. The proximate causes of extinction. In D. M. Raup and D. Jablonski (eds.), *Patterns and Processes in the History of Life*, pp. 259–276. Berlin: Springer Verlag.
- Simberloff, D., and N. Gotelli. 1984. Effects of insularization on plant–species richness in the prairie–forest ecotone. *Biological Conservation* 29:27–46.
- Smith, T. B., M. W. Bruford, and R. K. Wayne. 1993. The preservation of processes: The missing element of conservation programmes. *Biodiversity Letters* 1:164–167.
- Snyder, N. F. R., S. R. Derrickson, S. R. Beissinger, J. W. Wiley, T. B. Smith, W. D. Toone, and B. Miller. 1996. Limitations of captive breeding in endangered species

- recovery. *Conservation Biology* 10:338–348.
- Soulé, M. E. 1980. Thresholds for survival: Maintaining fitness and evolutionary potential. In M. E. Soulé and B. A. Wilcox (eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*, pp. 151–169. Sunderland, Mass.: Sinauer Associates.
- Soulé, M. E. 1987. *Viable Populations for Conservation*. Cambridge: Cambridge University Press.
- Soulé, M. E., M. Gilpin, W. Conway, and T. Foose. 1986. The millenium ark: How long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5:101–114.
- Soulé, M. E. and L. S. Mills. 1998. Population genetics—No need to isolate genetics science. *Science* 282:1658–1659.
- Soulé, M. E., and J. Terborgh. 1999. *Continental Conservation: Scientific Foundations for Regional Conservation Networks*. Washington, D.C.: Island Press.
- Terborgh, J., and B. Winter. 1980. Some causes of extinction. In M. E. Soulé and B. A. Wilcox (eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*, pp. 119–133. Sunderland, Mass.: Sinauer Associates.
- Thomas, C. D., and J. J. Lennon. 1999. Birds extend their ranges northwards. *Nature* 399:213.
- Thomas, C. D., and H. C. Mallorie. 1985. Rarity, species richness and conservation: Butterflies of the Atlas Mountains in Morocco. *Biological Conservation* 33:95–117.
- van Jaarsveld, A. S., S. Freitag, S. L. Chown, C. Muller, S. Koch, H. Hull, C. Belamy, M. Kruger, S. EndrodyYounga, M. W. Mansell, and C. H. Scholtz. 1998. Biodiversity assessment and conservation strategies. *Science* 279:2106–2108.
- WCMC. 1992. *Global Diversity: Status of the Earth's Living Resources*. London: Chapman & Hall.
- WCMC. 2000. *Global Biodiversity: Earth's Living Resources in the 21st Century*. Cambridge, U.K.: World Conservation Press.
- Williams, P. H. 1998. Key sites for conservation: Area-selection methods for biodiversity. In G. M. Mace, A. Balmford, and J. Ginsberg (eds.), *Conservation in a Changing World*, pp. 211–249. Cambridge: Cambridge University Press.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126–2128.

HUMAN ALTERATION OF FOOD WEBS

Research Priorities for Conservation and Management

Fiorenza Micheli, Gary A. Polis, P. Dee Boersma, Mark A. Hixon,
Elliott A. Norse, Paul V. R. Snelgrove, and Michael E. Soulé

MOST NATURAL FOOD WEBS HAVE BEEN ALTERED PROFOUNDLY through human activities (Botsford et al. 1997; Vitousek et al. 1997; Terborgh et al. 1999). Human perturbations of food-web interactions result from over-exploitation of species, particularly top predators; introduction of exotics; habitat destruction and fragmentation; and changes in resource availability through alteration of biogeochemical cycles, enhanced loadings of nutrients and organics, and "subsidies" of natural food webs through waste disposal or discarded fishery bycatch (see chapters 4, 5, 7, 9). Alterations of resource availability represent bottom-up perturbations of food-web dynamics, whereas removal or addition of consumers through hunting, fishing, species introductions, and habitat alteration represents a top-down perturbation. Top-down and bottom-up perturbations of natural food webs modify consumer-resource interactions, with subsequent impacts on population abundances, community structure and diversity, and ecosystem processes.

Biological conservation and management in the face of human impacts on whole ecosystems require an understanding of how consumer-resource interactions control populations and shape communities and a shift from focusing on single species to taking into account the complexity of ecological systems and interactions among their components (Lubchenco et al. 1991;

Christensen et al. 1996). This new tendency is exemplified by an increasing recognition among fishery managers that multispecies effects must be considered (NRC 1994; FAO 1997). Traditional, single-species fishery management has often failed to maintain populations of exploited species at sustainable levels (Ludwig et al. 1993). Classic examples include the collapse of the North Sea herring and mackerel stocks (Hempel 1978) and the northern cod (Walters and Maguire 1996). Part of the variability of commercial fish stocks, and the consequent uncertainty about their predicted trajectories, is caused by interactions with other species, which may, in turn, be impacted by harvesting conducted at multiple trophic levels (May et al. 1979; Yodzis 1994; Pauly et al. 1998). The present emphasis on marine reserves as tools for marine conservation and fisheries management exemplifies a shift in focus from an emphasis on single species to more holistic approaches to conservation and management (Roberts and Polunin 1993; Bonsauk 1996; Russ and Alcala 1996; Allison et al. 1998). These new approaches take into account the uncertainty of predictions about the combined effects of environmental variability and human impacts on species assemblages (Clark 1996; Lauck et al. 1998).

Decades of experimental studies have shown dramatic effects of consumer-resource interactions on populations and communities. Bottom-up effects of resources on consumers and top-down effects of consumers on other species in the community include a suite of direct and indirect pathways of interaction. Resource or prey availability controls the rates of population growth of their consumers, whereas predators exert direct effects on their prey abundance, size structure, and spatial distribution (Zaret 1980; Sih et al. 1985). Although even simple predator-prey systems can generate complex dynamics (McCauley et al. 1988), the uncertainty of predictions about resource and predation effects is further increased by responses mediated through other species in the community. Theoretical and empirical studies have shown that predators can influence community structure and diversity through indirect effects (Schoener 1993; Wootton 1993; Menge 1995; Abrams et al. 1996). In theory, there can be an almost unlimited number of different types of indirect effects and resulting dynamics (Hastings and Powell 1991; Abrams 1992), but experimental manipulations have revealed a more limited range of possibilities (Schoener 1993; Menge 1995; Abrams et al. 1996).

Knowledge of the role of consumer-resource interactions in regulating species dynamics and shaping natural communities has important conservation and management implications. Applications include:

- predicting the impacts of enhanced resource availability, predator removal, and species introduction on community structure;
- guiding predator manipulations aimed at decreasing mortality of an endangered or harvested species;

- controlling the abundance of pests and exotics;
- conserving or reintroducing top predators and keystone species with the aim of maintaining diversity or restoring the structure of altered communities through cascading effects;
- controlling the consequences of anthropogenic eutrophication of aquatic ecosystems through manipulation of the food-web structure (biomanipulation); and
- designing reserve networks to conserve whole assemblages and the interactions among their component species.

However, indirect effects and diffuse interactions among multiple species can cause unanticipated changes in community structure and nontarget effects of management interventions. Unraveling the tremendous complexity of the dynamics of multispecies communities is one of the main challenges confronting ecologists, conservation biologists, and environmental managers.

In this chapter, we identify the contributions of ecological studies of food-web interactions to conservation and management, and we highlight promising new research directions. First, we present the ecological theory of consumer-resource interactions and its applications to conservation and management. Second, we review the empirical evidence about the role of top-down and bottom-up forces in influencing the structure and dynamics of ecological communities. Third, we describe the importance of synthesizing experimental and monitoring data to develop generalizations that are more widely applicable, and we provide one example of such synthesis. Then we discuss whether and how to apply what we know about food-web interactions to real-world resource management. Finally, we propose some research priorities for the conservation and management of assemblages of interacting species.

Theory of Consumer-Resource Interactions

Ecological theory has produced a plethora of consumer-resource (i.e., predator-prey) models. One way of classifying these numerous contributions is on the basis of the number of species, or species groups, included in the models. Basic consumer-resource models, such as Lotka-Volterra's, focus on the dynamics of a two-species, enemy-victim system. The predator-prey interaction causes species abundances to cycle, with amplitudes determined by initial population abundances. A suite of biological mechanisms induces stability, including density-dependent (logistic) prey growth, density-dependent predator death rates or predator attack rates (interference among predators), physical refuges for the prey, the presence of an invulnerable life stage for the prey, and external sources of prey or predator recruits (open-system dynamics) (Gurney and Nisbet 1998). In contrast, enrichment is expected to destabilize predator-prey systems (the "paradox of enrichment," Rosenzweig 1971), although there is lit-

tle empirical evidence that real populations show the predicted instability in nutrient-rich environments (see Murdoch et al. 1998). Enemy-victim models such as Lotka-Volterra's and Nicholson-Bailey's, and later modifications of the original equations, have most commonly been applied to terrestrial systems, particularly in biological pest control (Hassell 1978; Murdoch et al. 1985; Waage and Mills 1992; Murdoch and Briggs 1996).

Predator-prey models of the Lotka-Volterra type typically isolate subsets of interacting species from a complex, multispecies ecosystem. Other species in the community are considered part of the environment and are not modeled explicitly. Thus, it is assumed that the dynamics of the target species are determined primarily by strong interactions with its prey or predator, and that links with other species in the community are weaker and less important in determining the system dynamics. However, Lotka-Volterra-type models have also been used to investigate the dynamics of multispecies assemblages. Species that use common resources in similar ways are grouped into trophic levels, which are assumed to act dynamically as populations. This approach was initiated by Hairston, Smith, and Slobodkin (1960) and further developed by Fretwell (1977) and Oksanen et al. (1981).

In Hairston et al.'s classic 1960 paper, food chains are composed of three trophic levels: plants, herbivores, and carnivores. Carnivores control herbivore populations, thereby releasing plants from top-down control and allowing accumulation of "green" biomass. Fretwell (1977) and Oksanen et al. (1981) expanded this approach to examine food-chain length and interactions along productivity gradients. Increasing productivity supports increasing numbers of trophic levels, which subsequently exert a top-down control on their prey and initiate cascading trophic interactions propagating down the food chain. At equilibrium, top-down control produces a stepped pattern of biomass increase along a productivity gradient, where top trophic levels and those even numbers of steps below are resource limited, whereas trophic levels odd numbers of steps below the top are limited by their consumers. Although linear food-chain models were originally developed with terrestrial systems in mind (Hairston et al. 1960; Fretwell 1977; Oksanen et al. 1981), they have been applied most commonly to aquatic systems (Persson et al. 1988, 1992; Crowder et al. 1988; Power 1990; Wootton and Power 1993; Brett and Goldman 1996, 1997).

Similar to linear food-chain models, trophic cascade models (Paine 1980) propose that predator-prey interactions are transmitted through food webs to cause variance in plant biomass and production (Carpenter et al. 1985). Trophic cascades are predation effects across multiple trophic levels resulting in inverse patterns of abundance or biomass across trophic levels of a food web. The trophic cascade hypothesis has been used to explain the ~50 percent

of observed variability in primary production of lakes that could not be attributed to variation in nutrient loading (Carpenter et al. 1985). Trophic cascades are also the basis for management manipulations of lake food webs referred to as biomanipulations (Shapiro et al. 1975; Gulati et al. 1990). Biomanipulation typically involves enhancement of piscivorous fish stocks or removal of planktivorous fish with the goal of decreasing predator control on large herbivorous zooplankton and increasing grazing of the phytoplankton. Thus, successful biomanipulation results in the biological control of one of the consequences of anthropogenic eutrophication, namely increased primary production (Carpenter and Kitchell 1992; Kitchell 1992).

Biological complexities that characterize many food webs can dampen trophic cascades and lead to weak or no top-down control. These include: (1) inedible prey or invulnerable life stages of prey (Murdoch 1966; Ehrlich and Birch 1967; McCauley et al. 1988; Leibold 1989; McQueen 1990; Strong 1992; Abrams 1993; Leibold et al. 1997); (2) complex interactions such as cannibalism, ontogenetic diet shifts, feeding on more than one trophic level (omnivory), and feeding on competitors (intraguild predation) (Mittelbach et al. 1988; Arditi and Ginzburg 1989; Strong 1992; Polis and Strong 1996; Holt and Polis 1997; McCann, Hastings, and Huxel 1998; McCann, Hastings, and Strong 1998); and (3) the fact that most food webs are not closed systems but systems that exchange resources and individuals with adjacent systems through nutrient and detritus input or loss, recruitment processes, and organism migration (Polis and Strong 1996; Polis et al. 1997; Huxel and McCann 1998). Inclusion of the above biological complexities in food-web models generates a range of possible community responses to variation in resource or consumer levels (table 3.1).

Basic consumer-resource and food-chain models focus on the dynamics of subsets of real food webs (figure 3.1). These systems are embedded in a more complex web of interactions (figure 3.2), which may affect the dynamics of the focal consumer-resource system (Polis and Strong 1996; Polis et al. 1997; Yodzis 1998, 2000). Attempts to model all trophic interactions within a community result in an overwhelming amount of possible interaction pathways. Can we safely ignore some of these pathways? Yodzis (1998) has tackled this question using the pelagic marine food web of the Benguela ecosystem, off South Africa (figure 3.2). Inclusion of all documented trophic interactions among the twenty-nine species of the food web yielded 203 direct links and millions of possible indirect pathways of interaction. He quantified the ecosystem response to the removal of one of the top carnivores in the system, South African fur seals, by examining predicted changes in the yield of the main commercial fisheries. This analysis shows that 44 percent of the 203 links can be eliminated from the model without altering the response of fish-

TABLE 3.1. Some Models of Top-Down and Bottom-Up Community Regulation

- *Hairston, Smith, and Slobodkin 1960*: Carnivores control herbivore populations, thereby releasing plants from top-down control and allowing accumulation of "green" biomass.
- *Murdoch 1966; McCauley et al. 1988; Leibold 1989; Strong 1992*: Prey defenses (e.g., inedible prey) dampen top-down effects.
- *Fretwell 1977; Oksanen et al. 1981*: Stepped pattern of biomass accrual along productivity gradients. Top trophic levels and those even numbers of steps below them are resource limited; trophic levels odd numbers of steps below the top one are predator limited.
- *Getz 1984; Arditi and Ginzburg 1989*: Interference among predators prevents their efficient exploitation of resources and leads to no top-down control. Biomass increases with increasing resource levels at all trophic levels. [AUTHOR: Please add Getz 1984 to Literature Cited]
- *Mittelbach et al. 1988*: Ontogenetic diet shifts. Predators cannot track resources because resource increases influence only one life stage, leading to weak top-down effects.
- *McQueen 1990*: Bottom-up control is stronger at base of food web; top-down control is stronger at higher trophic levels. Trophic cascades attenuate before reaching plants.
- *Polis and Strong 1996*: Complex interactions among components of food webs dampen top-down control. Multichannel omnivory can promote top-down regulation when top consumers are subsidized by external resources. Thus, omnivory can both dampen and enhance top-down effects.
- *Leibold et al. 1997*: Species replacement through time (predation selects for defended prey). Weak top-down effects in the long-term.
- *McCann, Hastings, and Strong 1998*: Intraspecific interference affecting consumer population growth rates dampen top-down effects. Increased productivity results in increased plant biomass, whereas consumer biomass shows a modest increase.
- *Huxel and McCann 1998*: Allochthonous resource input weakens top-down control.

Source: Modified from M. E. Power, "Top-Down and Bottom-Up Forces in Food Webs: Do Plants Have Primacy?" *Ecology* 73 (1992): 733–746.

ery yields to seal culling, suggesting that some simplification of the system is possible. Even such simplification leaves 112 direct consumer-resource links potentially influencing the system response to perturbation, still a tremendously complex system. Further modeling and empirical work should determine how much detail is needed to describe the dynamics of whole communities and under what circumstances complex systems yield predictable responses to perturbation (e.g., Terborgh et al. 1999).

Empirical Evidence: How Top-Down and Bottom-Up Forces Influence Ecological Communities

Experiments consisting of altering resource levels and adding or removing consumers have shown that consumer-resource interactions can play a critical role in regulating populations and shaping communities and have eluci-

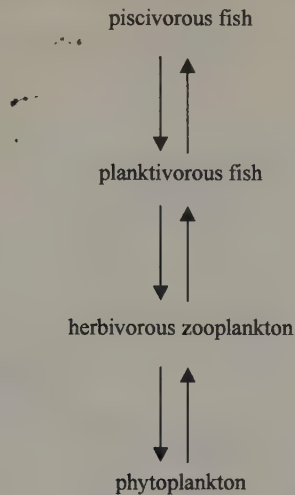


FIGURE 3.1. A simplified food chain comprising four trophic levels: piscivorous fish (e.g., tuna), planktivorous fish (e.g., anchovy), herbivorous zooplankton (e.g., copepod crustaceans), and phytoplankton.

dated direct and indirect mechanisms underlying predation effects (e.g., Sih et al. 1985; Schoener 1993; Wootton 1993; Menge 1995). Unfortunately, controlled manipulative experiments often cannot be conducted over the spatial and temporal scales relevant to biological conservation and management. Despite the difficulty of interpreting observed patterns in the lack of replication and controlled reference conditions, “natural” experiments provide an opportunity to examine the consequences of food-web alterations at large scales (e.g., Terborgh et al. 1999). The alteration of resource availability through nutrient enrichment or food-web subsidies, the widespread decline or loss of top consumers caused by fishing and hunting, and the introduction of predators to new areas are large-scale manipulations of food-web structure and consumer-resource interactions.

Human activities result in the production of nutrients and organic matter that can fuel natural food webs and alter abundances and interactions of species or whole trophic levels. In particular, industrial and agricultural activities add to terrestrial systems at least as much fixed nitrogen as all natural sources combined (Vitousek et al. 1997). Nitrogenous compounds from industrial activities, agriculture, and sewage, reach rivers, lakes, and oceans through groundwater and atmospheric discharge. Enhanced nitrogen input generally results in increased primary productivity, decreased biological diversity, and changes in plant community composition in both terrestrial and aquatic ecosystems (Schindler 1974; Tilman 1987; Nixon 1995; Jeffries

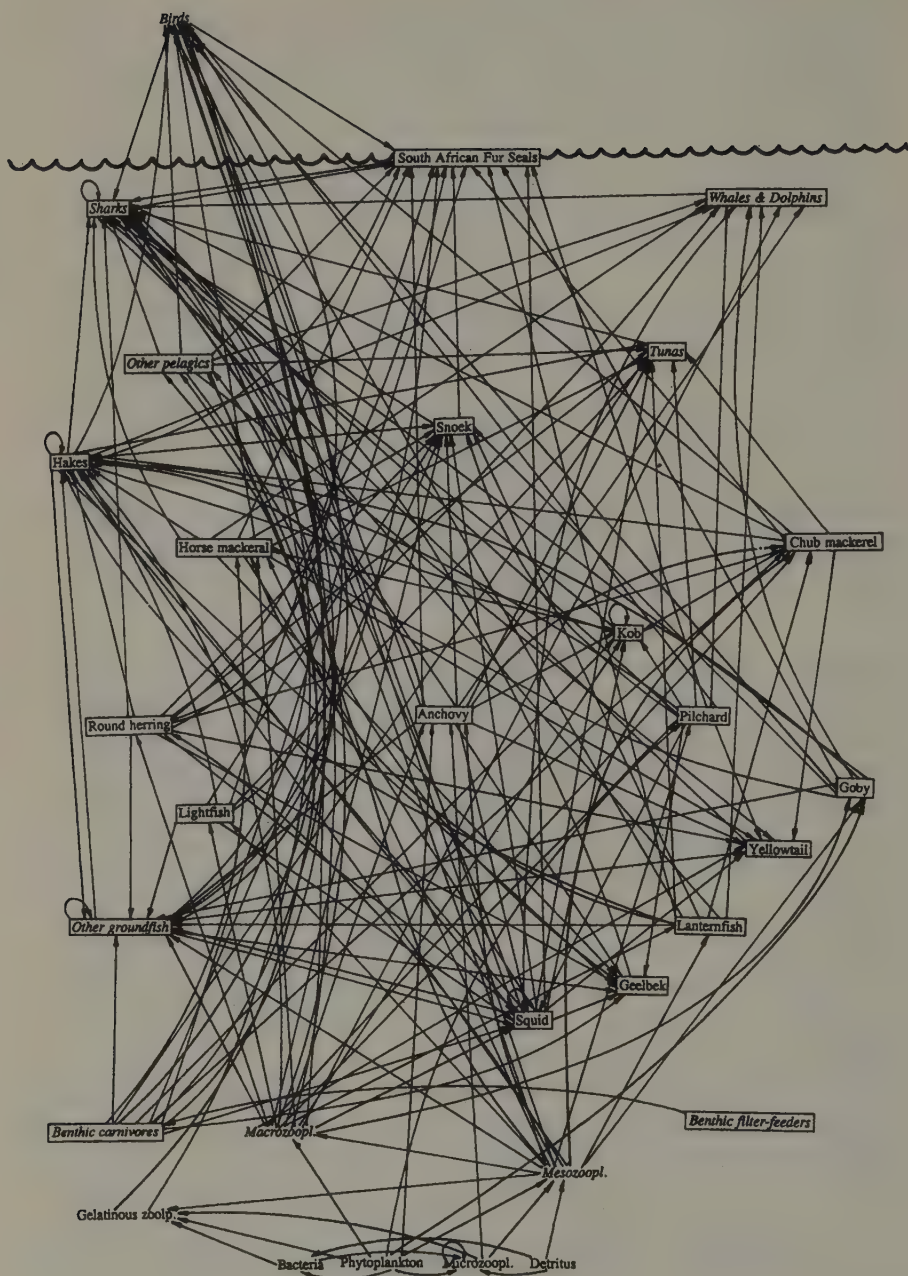


FIGURE 3.2. The Benguela ecosystem food web (from Yodzis 1998, reproduced with author's permission). The species and species groups are embedded in a complex web of trophic and nontrophic interactions.

and Maron 1997). Such increased primary productivity can support greater abundance and biomass of higher trophic levels (Oksanen et al. 1981; McNaughton et al. 1989). However, anthropogenic nutrient enrichment frequently disrupts food-web interactions, causing ungrazed primary production to accumulate in the focal system or in adjacent ecosystems. The consequences of anthropogenic eutrophication, such as algal and microbial blooms (including toxic species), hypoxic/anoxic conditions of the water column, and mass mortality of fish and invertebrates, are particularly widespread and worrisome in coastal marine ecosystems (Hallegraeff 1993; Turner and Rabalais 1994; Nixon 1995; chapter 7).

A range of human activities produces waste that can subsidize natural food webs. For example, trash dumps and the bycatch discarded by commercial fisheries can provide important resources for scavengers and opportunistic predators, including fish, crabs, seabirds, and raptors (Dayton et al. 1995; Garthe et al. 1996; Blanco 1997), which may in turn control populations of competitors or prey and influence community structure. We still know very little about the impacts of different types of resource subsidies on natural ecosystems, how such impacts vary across spatial scales (from the local effects of waste dumping to the global effects of the alteration of the nitrogen and carbon cycles), and how the enhanced productivity supported by the added resources alters food-web dynamics.

The decline and collapse of top carnivores provide ample evidence that predation can structure aquatic and terrestrial communities (Crowder et al. 1996; Terborgh et al. 1999). One of the best-documented case studies is the sea otter–sea urchin–kelp trophic cascade occurring in North American coastal marine habitats (Estes and Palmisano 1974; Estes et al. 1998). Hunting reduced sea otters to a number of widely scattered remnant populations along the northwestern coast of the United States. The absence of sea otters often is associated with an abundance of sea urchins, which overgraze large benthic algae, including kelps (Estes and Palmisano 1974). In recent years, increased predation by killer whales on sea otters, possibly caused by a decline in the pelagic prey of killer whales, may have led to sea otter decline and increased sea urchin abundance and overgrazing of kelp (Estes et al. 1998). In lakes, experimental or fisheries removal of piscivorous fish can cause trophic cascades, leading to increased abundance of planktivorous fish, alterations of the size structure and species composition of the zooplankton, and increased phytoplankton biomass (Carpenter et al. 1985; Kitchell 1992; Carpenter and Kitchell 1993).

McLaren and Peterson (1994) documented a compelling example of a terrestrial trophic cascade on Isle Royale, Michigan, USA. Wolves control moose populations, which in turn influence tree growth rates. When wolves were

rare, moose abundances increased and the growth rates of balsam fir were depressed. Hunting, combined with habitat destruction and fragmentation, has drastically reduced the abundance and geographical range of many top carnivores, including wolves, bears, coyotes, cougars, lions, and tigers. In North America, reduction or elimination of top predators has resulted in the "mesopredator release" of other small or midsized predators, such as foxes, skunks, raccoons, and feral and domestic cats (Soulé et al. 1988), thereby altering food-web dynamics and community structure. For example, the decline and disappearance of coyotes in landscapes fragmented by development affects the distribution and abundance of smaller carnivores and the persistence of their avian prey (Crooks and Soulé 1999). In suburban areas and parklands of North America, where hunting eliminated top carnivores in the past but is now prohibited, mammals that were part of the top carnivore prey pool, like deer, have increased in numbers, in some cases becoming road hazards and overbrowsing the vegetation (McShea et al. 1997).

In pelagic marine ecosystems, there are many examples of declines of top predators accompanied by species replacement at the same trophic level or in changes of the prey community at the next trophic level. Hunting of blue whales around Antarctica was followed by increased abundance of other species feeding on krill, including minke whales, crab-eater seals, and penguins (Laws 1984; Brownell et al. 1989). On Georges Bank, off the New England coast, small elasmobranchs (mainly dogfish sharks and skates) have increased in abundance following the collapse of the stocks of large gadid fishes such as haddock and cod. This switch in species dominance is likely due to increased prey availability for the elasmobranchs caused by the decline of the piscivorous gadid and flounder species (Fogarty and Murawski 1998). Extensive removal of large sharks off South Africa led to increased abundances of small sharks, on which the large sharks preyed, and to reductions of commercial fish yields (van der Elst 1979). In the North Sea, decline in the herring and mackerel stocks resulted in increased catch of their prey, mostly smaller fish including sand lance, sprat, and Norway pout (Hempel 1978). In contrast, the decline or depletion of some marine apex predators, including great auks, Steller's sea cows, and gray whales, appears to have caused only subtle changes in populations of their prey and competitors (Boersma and Moore in press). In these case studies, it is not known how other food-web components—for example, plankton or benthos—responded to predator decline.

Marine reserves—portions of the coastline protected from fishing and other human disturbance—constitute large-scale human-exclusion experiments. As such, they present an invaluable opportunity to determine the impacts of food-web alterations on marine communities. In the Las Cruces marine reserve, cen-

tral Chile, the predatory gastropod *Concholepas concholepas* ("loco") increased in abundance within the reserve compared to adjacent areas where it was harvested. Increased predation by *Concholepas* on its prey, particularly mussels, led to the almost complete elimination of mussel beds, which were replaced by barnacles and algae (Castilla 1999). Increased abundance of predatory fishes within no-take marine reserves in Spain and East Africa has been linked to increased predation on sea urchins, decreased urchin abundance, changes in population size structure, and a proliferation of fleshy algae (Sala and Zabala 1996; McClanahan et al. 1999).

Introductions of exotic predators provide further evidence of the potential for top-down and bottom-up effects to influence communities and ecosystems. Intentional introductions of fishery species to lakes have had devastating consequences for native communities. The introduction of the peacock bass to Gatun Lake, Panama, led to the loss of several native species of fish and to a simplification of the food web (Zaret and Paine 1973). Similarly, the introduction of the Nile perch to Lake Victoria, East Africa, has profoundly altered the native fish community and caused the loss of many endemic species of cyclid fishes (Barel et al. 1985; Kitchell et al. 1997). The accidental introduction of the ctenophore *Mnemiopsis leidyi*, a consumer of zooplankton and juvenile fish, to the Black Sea has caused further decline and loss of several species of crustacean zooplankton and planktivorous fish in a system already heavily impacted by increased nutrient loading, chemical pollution, and fisheries exploitation (Zaitsev 1992).

The introduction of exotic predators to predator-free islands provides evidence for top-down regulation of some terrestrial communities. For example, the accidental introduction of the brown tree snake to Guam led to the extinction of several species of native birds (Savidge 1987). Similarly, the introductions of foxes to the Alaskan Islands and mongoose to tropical Pacific islands have contributed to the collapse of native fauna (King 1984; Bailey 1993). Exotics may also influence ecosystem processes, altering resource availability for other species and the structure and dynamics of the whole ecosystem. One compelling example is the invasion of the nitrogen-fixing tree *Myrica faya* in Hawaii. The establishment of *Myrica faya* in newly formed volcanic habitats can lead to a rapid increase of the biologically available nitrogen in nutrient-poor volcanic soils, causing dramatic changes of the plant and soil communities and favoring subsequent invasions by non-native organisms (Vitousek and Walker 1989).

Synthesis of Experimental and Monitoring Data

Experimental predator or resource manipulations and large-scale "natural" experiments associated with the decline or introduction of predators, nutrient

enrichment, and food-web subsidies provide crucial information about the types of community changes caused by food-web alterations and point to urgent research priorities for conservation and management.

Fundamental questions concern how commonly different community responses occur and what conditions are more likely to lead to a particular type of community response. Are all systems unique? Can the changes observed in one system be expected in other systems? Syntheses of experimental and monitoring data can produce generalizations about community responses to food-web alterations and yield predictions about the most likely outcomes of future perturbations and management interventions. Unfortunately, the plethora of empirical data documenting food-web effects in experimental and natural systems have rarely been synthesized to test whether general responses exist. For an example of such quantitative synthesis, we focus on generalizations about trophic cascades as one mechanism leading to community changes following the addition or removal of consumers in aquatic ecosystems.

Trophic cascades (predation effects across multiple trophic levels resulting in inverse patterns of abundance or biomass across a food web) have received much attention for their potential to spread alterations in consumer levels across an entire food web. Thus, loss or introduction of predators may impact the whole community through cascading trophic interactions. In addition, trophic cascades have management applications as a means of controlling the productivity and biomass of the phytoplankton in waters subject to anthropogenic nutrient loading (Shapiro et al. 1975; Gulati et al. 1990; Kitchell 1992).

Trophic cascades have been documented in a variety of terrestrial and aquatic ecosystems, including temperate and tropical reefs, rocky intertidal communities, streams, lakes, and terrestrial insect communities in the tropics (Power 1990; Wootton 1995; Spiller and Schoener 1994; Hixon 1997; Letourneau and Dyer 1998; Pace et al. 1999; Pinnegar et al. 2000; and references in the preceding "Empirical Evidence" section). Most documented cascades occur among a few of the species in the community, particularly in terrestrial systems (Polis 1999; Persson 1999). However, trophic cascades influencing the structure and dynamics of whole communities occur in aquatic ecosystems (e.g., Estes and Palmisano 1974; Power 1990; Carpenter and Kitchell 1993; Shiimoto et al. 1997; Estes et al. 1998). Thus, food-web alterations can initiate cascading trophic interactions influencing the structure of aquatic communities. How commonly do trophic cascades occur, and in what conditions are they more likely to occur?

Syntheses conducted in lakes, marine pelagic ecosystems, and rocky intertidal communities indicate that trophic cascades are uncommon in those systems. In a meta-analysis of predator (fish) manipulations conducted in lakes, Brett and Goldman (1997) found that fish exerted a strong control on their

prey, the zooplankton, but phytoplankton biomass exhibited weak responses to fish manipulation. In a more extensive analysis, phytoplankton responded strongly to fish manipulation in approximately one-third of fifty-four enclosure or pond experiments and showed weak responses in the others (Brett and Goldman 1996).

Meta-analyses of data from manipulations of nutrients and consumers conducted in marine mesocosms and long-term monitoring of nutrients, phytoplankton, zooplankton, and zooplanktivorous fish abundance in open pelagic ecosystems indicated that trophic cascades are uncommon in marine pelagic food webs (Micheli 1999). In particular, of the twenty open marine systems included in this analysis, only one exhibited an inverse pattern in biomass across three trophic levels. A ten-year time series of phytoplankton, zooplankton, and a planktivorous predator, the pink salmon *Oncorhynchus gorbuscha*, from the subarctic Pacific Ocean showed that interannual variation in salmon abundance was inversely related to zooplankton biomass and positively related to phytoplankton biomass (Shiomoto et al. 1997).

In general, year-to-year fluctuations in zooplankton biomass were negatively correlated with fish, indicating that fish predation may control zooplankton biomass. In contrast, the zooplankton and the phytoplankton were not significantly correlated, indicating that fish predation does not commonly control the biomass of primary producers in these pelagic ecosystems (Micheli 1999). An important implication is that biomanipulations are unlikely to control phytoplankton production and biomass in the coastal marine environment. Reductions of anthropogenic nutrient loading to coastal waters may be the only means of controlling marine eutrophication.

Whole-lake experiments suggest that trophic cascades may be enhanced under nutrient-rich conditions (Pace et al. 1999). This result has important implications because most aquatic systems are subjected to simultaneous food-web alterations, through fishing and introduction of exotic species, and to increased nutrient loading from agricultural activities and coastal development. Food-web manipulations conducted in marine mesocosms suggest that nutrient enrichment may favor trophic cascades also in marine food webs. Overall, there was a statistically significant increase in phytoplankton biomass following the addition of planktivorous fishes in mesocosms enriched with nitrogen but not in mesocosms with no nutrients added (Micheli 1999). However, patterns from open marine systems do not support this hypothesis: the only system where trophic cascades occurred had the lowest productivity among the twenty systems in the data set (Micheli, unpublished data).

In a survey of direct and indirect effects in experimental manipulations of twenty-three marine rocky intertidal food webs, Menge (1995) found that indirect effects accounted for a large proportion of the community changes caused by manipulations (24 to 61 percent, mean \approx 40 percent). Nearly half of all indirect effects (total = 565) resulted from manipulations of predators. In

these food webs, 6.5 percent of all indirect effects were trophic cascades. The most frequent types of indirect effects were keystone predation (when a predator's consumption of a prey increases the abundance of the prey competitors: 35 percent of all indirect effects) and apparent competition (when species share a common predator and increased abundance of one species enhances predation on the other species: 25 percent).

In conclusion, trophic cascades can have important effects on community structure and species dynamics (see the "Empirical Evidence" section) but appear to be more common in some ecosystem types—such as shallow marine benthic communities, small lakes, and vertebrate terrestrial systems—and in the presence of intense anthropogenic disturbance (Carpenter et al. 1985; Terborgh et al. 1999; Pinnegar et al. 2000). Our present perception may reflect biases in the focus and time frames of the studies conducted to date. For example, shallow benthic marine communities are more accessible and amenable to experimental manipulations than offshore pelagic ecosystems (Pinnegar et al. 2000). In addition, large terrestrial and aquatic predators have been decimated through hunting, fishing, and habitat destruction long before the start of the monitoring programs and ecological studies with which we are attempting to detect the community consequences of predator removal (e.g., Jackson 1997). Determining what conditions lead to trophic cascades, how commonly they occur in different types of ecosystems, and the temporal and spatial scales at which food-web perturbations alter community structure and interactions is an important research priority.

Conclusions

There is ample experimental and correlative evidence that consumer-resource interactions play an important role in regulating population dynamics, community structure, and diversity. Potential applications include:

- predicting the impacts of food-web alterations on population and community dynamics;
- conserving top predators and keystone species, preventing competitive displacement of species, and maintaining diversity;
- manipulating consumers and resources to restore community structure and ecosystem processes;
- conserving species or species groups that effectively control pests and exotic invaders;
- designing reserve networks to conserve whole assemblages and the interactions among their component species; and
- controlling anthropogenic eutrophication of aquatic ecosystems through biomanipulation of food webs.

Do we know enough about bottom-up and top-down regulation of natural communities to predict change and implement these conservation and management strategies successfully?

Theory and data indicate that there is considerable indeterminacy about the type, magnitude, and direction of community changes following food-web alterations. Perturbations caused by the addition or removal of a resource or of a consumer species can cause both direct and indirect effects and result in a large suite of possible outcomes (Bender et al. 1984; Yodzis 1988; Abrams 1993; Wootton 1993). Because of the inherent variability of ecological processes and the fragmentary data available, we will never be able to fully explain and predict species dynamics and community change. Management of species and ecosystems in the face of uncertainty requires implementation of the precautionary principle (FAO 1995; Lauck et al. 1998) and of adaptive management (Walters 1986; Parma et al. 1998). Uncertainty about the consequences of food-web alterations in complex, multispecies communities is an additional reason to use precautionary and adaptive approaches in conservation and management. Nevertheless, a better understanding of processes structuring communities, including food-web interactions, could only help reduce some of the uncertainty.

Perhaps the main challenge in applying food-web research to conservation is how to deal with the multitude of possible direct and indirect pathways of interactions among species. One approach is to focus on subsets of species linked through strong interactions and weakly linked to other species in the system (community "modules," Holt 1996). Simplifying complex communities to smaller subsets of strong interactors that largely drive community dynamics allows a mechanistic understanding of consumer-resource interactions and has a strong theoretical basis in a plethora of predator-prey models. However, we still know very little about the relative frequencies of strong and weak interactions in natural communities (Power et al. 1996). Direct quantification of interaction strength in two marine and one terrestrial community indicated that most interactions were weak, with a few strong interactions (Paine 1992; Power et al. 1996), but broader comparisons are needed before any generalization is possible.

The presence of strong interactors within communities, such as keystone predators, has potentially broad applicability in conservation because it allows focusing monitoring and management on key species that regulate the structure and diversity of the whole community. To date, there are no general guidelines about the traits that characterize keystones or the types of communities where they are more likely to occur (Mills et al. 1993; Power et al. 1996). Identifying the species that are strong interactors in different communities, as well as the context where species are most likely to be strong interactors, is an

important research priority for the coming decade. However, ample evidence suggests that the top predators targeted by hunting and fishing tend to exert strong top-down effects and that immediate action should be taken to protect top predators and prevent further disruption of natural food webs.

Attempts to model, manipulate, or measure all possible interactions in a food web quickly exceed data availability and our ability to relate community patterns to the processes that underlie them. Aggregation of species into trophic levels is one means of simplifying complex communities while including multiple species, but it can overlook important biological complexities. For example, intratrophic interference, nontrophic interactions, and long-term species replacement result in community patterns that are not predicted by linear food-chain models (table 3.1). Models of intermediate complexity and determination of what key processes should be included for different ecosystems seem the most promising research directions for producing theory and guidelines for conservation and management. The added realism renders models less general but more applicable to particular systems (Murdoch and Briggs 1996).

The community-wide consequences of fishery collapses, loss of top carnivores from terrestrial systems, introduction of exotic species, and anthropogenic nutrient enrichment of ecosystems indicate that the removal or addition of consumers and resources generally influences prey at the next lower trophic level and the species that directly use the resource. Frequently, species replacement occurs within a trophic level. In some cases, effects can also influence the whole community through trophic and nontrophic interactions cascading through the food web. Establishing the generality of these trends and identifying the key processes underlying community responses to food-web perturbations are urgent research priorities.

Research Priorities

The following priorities and their components are outlined in box 3.1.

Produce Generalizations about Species and Community Responses to Food-Web Alteration

Theory and experiments have shown that food-web alterations influence communities through a range of direct and indirect pathways of interactions, which result in a large suite of possible outcomes (Bender et al. 1984; Yodzis 1988; Abrams 1993; Wootton 1993). Yet recent syntheses of data suggest that some generalization may be possible. In freshwater and marine pelagic food webs, alterations of resource and consumer levels cause similar general patterns of community change (Brett and Goldman 1996, 1997; Micheli 1999). In marine rocky intertidal food webs, experimental manipu-

lations caused several types of indirect effects, but approximately 60 percent of indirect effects were either keystone predation or apparent competition (Menge 1995). "Natural" experiments provided by the variation in space and time of human impacts (e.g., Estes et al. 1998; Crooks and Soulé 1999; Terborgh et al. 1999) represent invaluable opportunities to examine food-web responses to bottom-up and top-down forces over large scales and compare responses across systems. Syntheses of existing data may produce generalizations about community responses to food-web alterations and generate predictions about the likelihood of different effects of future perturbations or management interventions.

Determine Level of Resolution of Community Representation

There is an urgent need to determine how much detail is necessary to detect change and predict community dynamics in the face of environmental variability and human impacts. The difficulty and costs of modeling and monitoring species dynamics and interactions within complex food webs increase quickly with increasing resolution of models and sampling. Some form of simplification is necessary. This is typically achieved by focusing on small groups of interacting species or by lumping species into trophic levels or functional groups. Simulations, resampling of existing data, and investigation of the effects of aggregating species-level data into broader categories are promising avenues for determining how much detail can be omitted from food-web models and for producing guidelines for monitoring multispecies assemblages (e.g., Frost et al. 1995; Cottingham and Carpenter 1998; Yodzis 1998).

Understand the Effects of Nutrient and Organic Enrichment of Ecosystems

The availability of resources to species at all trophic levels of natural food webs is altered through a variety of human activities. Human alteration of the availability of nutrients, detritus, and prey to producers and consumers is a widespread phenomenon, but it includes a variety of types of alteration, occurring over local to global scales. Determining how different types and scales of subsidies influence food-web interactions, community structure, and ecosystem processes is an urgent research priority in the face of the ever increasing human production of pollutants and waste.

Link Pattern and Process to Understand Mechanisms Underlying Food-Web Dynamics

A better understanding of the processes underlying observed community dynamics would greatly improve conservation and management of aquatic

BOX 3.1. Research Priorities for Food-Web Conservation and Management

Produce Generalizations about Species and Community Responses to Food-Web Alteration

- *1. Characterize community responses to food-web alterations and determine which conditions are more likely to lead to a particular type of community response.
2. Determine unique vs. general responses to food-web perturbation.
3. Relate the strength and effects of consumer-resource interactions to environmental gradients in productivity and disturbance.
4. Explore how systems of increasing complexity respond to perturbation and determine under what circumstances complex systems may yield predictable responses to perturbation.
5. Investigate the separate and joint effects of different types of food-web perturbations.

Determine Level of Resolution of Community Representation

- *1. Determine how many species and interactions can be omitted from monitoring and models and what level of aggregation still allows accurate representation of community dynamics.
2. Establish the relative frequencies of strong and weak interactions in natural ecosystems.
3. Investigate what traits characterize strong interactors and keystone species.

Understand the Effects of Nutrient and Organic Enrichment of Ecosystems

- *1. Determine how different types of subsidies influence food-web interactions, community structure, and ecosystem processes.

ecosystems. One approach is to develop mechanistic models that represent alternative views of the processes driving food-web dynamics, and to compare model predictions to observed patterns. Confidence in alternative models is built through comparisons of model predictions to data, thereby linking observed patterns of community change to specific mechanisms of consumer-resource interactions. For example, Shea et al. (1998) proposed testing alternative process-based models against population time series to improve population management in conservation, fisheries management, and pest control. Similarly, Kendall et al. (1999) combined mechanistic models and time-series statistical models to elucidate the processes underlying population cycles. McCann, Hastings, and Strong (1998) compared predic-

2. Investigate how nutrient and organic matter subsidies influence food-web dynamics in ecosystems already subjected to other perturbations, including overexploitation, habitat degradation, and climate change.
3. Explore how the effects of food-web subsidies vary between natural sources (e.g., oceanic upwelling, litter fall, bird guano) and anthropogenic sources (e.g., sewage and fertilizers, urban waste, discarded fisheries bycatch).
4. Evaluate how the effects of resource alteration vary among local, regional, and global scales.

Link Pattern and Process to Understand Mechanisms Underlying Food-Web Dynamics

1. Link alternative models of consumer-resource interactions to observed patterns of community change.
- *2. Develop models that include the influence of human activities on community and ecosystem dynamics and explore alternative conservation and management scenarios before they are implemented.

Determine Scale of Interactions and Food-Web Boundaries

- *1. Determine the relevant food-web components influencing community structure and diversity.
- *2. Investigate the effects of the movement of energy, matter, and organisms across community and ecosystem boundaries on food-web dynamics.
- *3. Establish the temporal and spatial scales over which community change can be detected.
4. Explore how local, regional, and global food-web perturbations influence each other.

Note: Asterisks denote the six highest priorities for the current decade.

tions of food-web models that include different forms of interference among consumers to patterns of biomass change at different trophic levels of lake food webs. Modeling also can be used to simulate scenarios that cannot be simultaneously realized in practice, allowing exploration of the effects of species addition and deletion, of single vs. multiple perturbations, and of different management strategies.

Determine Scale of Interactions and Food-Web Boundaries

A largely unexplored area is that of how delimiting food webs and ecosystems using different criteria and over different spatial and temporal scales may influence conclusions about the community and ecosystem conse-

quences of food-web interactions (e.g., Polis et al. 1997). For example, our understanding of above-ground plant-insect interactions and marine plankton dynamics was dramatically changed by including soil (Strong 1999) and microbial (Pomeroy 1974) communities in these food webs. Similarly, the dynamics of intertidal marine communities and terrestrial communities on small islands are largely influenced by oceanic input of larvae (Roughgarden et al. 1988) and detritus (Bustamante et al. 1995; Polis and Hurd 1996). Historical and paleontological data indicate that coral reef communities have been impacted and modified by fishing and other human activities well before the start of the monitoring programs with which we attempt to detect temporal change (Jackson 1997). Scale and boundary issues are relevant to a suite of conservation and management applications, such as designing networks of reserves, managing watersheds and coastal areas, and determining whether species assemblages are being modified by human disturbances. Tackling scale issues will require conducting research at multiple scales, using a diverse set of perspectives and approaches, and establishing interdisciplinary collaborations.

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LITERATURE CITED

- Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: Unusual effects of interacting foraging adaptations. *American Naturalist* 140: 573–600.
- Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. *American Naturalist* 141: 351–371.
- Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. In G. A. Polis and K. O. Winemiller (eds.), *Food Webs—Integration of Patterns and Dynamics*, pp. 371–395. New York: Chapman and Hall.
- Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* 8: 79–92.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: Ratio dependence. *Journal of Theoretical Biology* 139: 311–326.
- Bailey, E. P. 1993. *Introduction of foxes to Alaskan islands—History, effects on avifauna, and revocation*. Resource publication 193. Washington, D.C.: U.S. Department of Interior, Fish and Wildlife Service.

- Barel, C. D. N., R. Dorit, P. H. Greenwood, G. Fryer, N. Hughes, P. B. N. Jackson, H. Kawanabe, R. H. Lowe-McConnell, M. Nagoshi, A. J. Ribbink, E. Trewavas, F. Witte, and K. Yamaoka. 1985. Destruction of fisheries in Africa's lakes. *Nature* 315: 19–20.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: Theory and practice. *Ecology* 65: 1–13.
- Blanco, G. 1997. Role of refuse as food for migrant, floater and breeding black kites (*Milvus migrans*). *Journal of Raptor Research* 31: 71–76.
- Boersma, P.D., and S. E. Moore. In press. Seabirds and marine mammals: Political keystones. In P. Kareiva and S. Levin (eds.), *The Importance of Species: Perspectives on Expandability and Triage*.
- Bonsauk, J. A. 1996. Maintenance and recovery of reef fishery productivity. In N. V. C. Polunin and C.M. Roberts (eds.), *Management of Reef Fisheries*, pp. 283–313. London: Chapman and Hall.
- Botsford, L.W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277: 509–515.
- Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. *Proceedings of the National Academy of Science of the USA* 93: 7723–7726.
- Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. *Science* 275: 384–386.
- Brownell, R. L. Jr., K. Ralls, and W. F. Perrin. 1989. The plight of the forgotten whales. *Oceanus* 32: 5–20.
- Bustamante, R. H., G. M. Branch, and S. Eekhout. 1995. Maintenance of an exceptional intertidal grazer biomass in South Africa: Subsidy by subtidal kelps. *Ecology* 76: 2314–2329.
- Carpenter, S. R., and J. F. Kitchell. 1992. Trophic cascade and biomanipulation: Interface of research and management. *Limnology and Oceanography* 37: 208–213.
- Carpenter, S. R., and J. F. Kitchell (eds.). 1993. *The Trophic Cascade in Lakes*. Cambridge: Cambridge University Press.
- Carpenter, S. R., J. F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 38: 764–769.
- Castilla, J. C. 1999. Coastal marine communities: Trends and perspectives from human-exclusion experiments. *Trends in Ecology and Evolution* 14: 280–283.
- Christensen, N.L., A. M. Bartuska, J. H. Brown, et al. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecological Applications* 6: 665–691.
- Clark, C. W. 1996. Marine reserves and the precautionary management of fisheries. *Ecological Applications* 6: 369–370.
- Cottingham, K. L., and S. R. Carpenter. 1998. Population, community, and ecosystem variates as ecological indicators: Phytoplankton responses to whole-lake enrichment. *Ecological Applications* 8: 508–530.
- Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563–566.
- Crowder, L. B., R. W. Drenner, W. C. Kerfoot, D. J. McQueen, E. L. Mills, U. Sommer,

- C. Spencer, and M. J. Vanni. 1988. Food web interactions in lakes. In S. R. Carpenter (ed.), *Complex Interactions in Lake Ecosystems*, pp. 141–160. New York: Springer-Verlag.
- Crowder, L. B., D. P. Reagan, and D. W. Freckman. 1996. Food web dynamics and applied problems. In G. A. Polis and K. O. Winemiller (eds.), *Food Webs—Integration of Patterns and Dynamics*, pp. 327–336. New York: Chapman and Hall.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation* 5: 205–232.
- Ehrlich, P. R., and L. C. Birch. 1967. The “balance of nature” and “population control.” *American Naturalist* 101: 97–107.
- Estes, J. A., and J. F. Palmisano. 1974. Sea otters: Their role in structuring nearshore communities. *Science* 185: 1058–1060.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473–476.
- FAO (Food and Agriculture Organization of the United Nations). 1995. *Draft guidelines on the precautionary approach to capture fisheries*. Report of the technical consultation on the Precautionary Approach to Capture Fisheries, Lysekil, Sweden, June 6–13, 1995. Rome: FAO and Swedish National Board of Fisheries.
- FAO (Food and Agriculture Organization of the United Nations). 1997. *Technical guidelines for responsible fisheries*. Rome: FAO.
- Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine systems—Fishery impacts on Georges Bank. *Ecological Applications* 8: S6–S22.
- Fretwell, S. D. 1977. The regulation of plant communities by the food chains exploiting them. *Perspectives in Biology and Medicine* 20: 169–185.
- Frost, T. M., S. R. Carpenter, A. R. Ives, and T. K. Kratz. 1995. Species compensation and complementarity in ecosystem function. In C. G. Jones and J. H. Lawton (eds.), *Linking Species and Ecosystems*, pp. 224–240. New York: Chapman and Hall.
- Garthe, S., C. J. Camphuysen, and R. W. Furness. 1996. Amounts of discards by commercial fisheries and their significance as food for birds in the North Sea. *Marine Ecology Progress Series* 136: 1–11.
- Getz, W. M. 1984. Population dynamics: A per capita resource approach. *Journal of Theoretical Biology* 108: 623–643.
- Gulati, R. D., E. H. R. R. Lammens, M.-L. Meijer, and E. van Donk (eds.). 1990. *Bio-manipulation—Tool for water management*. Dordrecht: Kluwer Press.
- Gurney, W. S. C., and R. M. Nisbet. 1998. *Ecological Dynamics*. New York: Oxford University Press.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94: 421–425.
- Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32: 79–99.
- Hassell, M. P. 1978. *The Dynamics of Arthropod Predator-Prey Systems*. Princeton, N.J.: Princeton University Press.

- Hastings, A., and T. Powell. 1991. Chaos in a three-species food chain. *Ecology* 72: 896–903.
- Hempel, G. 1978. North Sea fisheries and fish stocks—A review of recent changes. *Rapports et Proces Verbaux des Reunions du Conseil Permanent International pour l'Exploration de la Mer* 173: 145–167.
- Hixon, M. A. 1997. The effects of reef fishes on corals and algae. In C. Birkeland (ed.), *Life and Death on Coral Reef*, pp. 230–248. New York: Chapman and Hall.
- Holt, R. D. 1996. Community modules. In M. Begon, A. Gange, and V. Brown (eds.), *Multitrophic Interactions*, pp. 333–350. London: Chapman and Hall.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* 149: 745–764.
- Huxel, G. R., and K. McCann. 1998. Food web stability: The influence of trophic flows across habitats. *American Naturalist* 152: 460–469.
- Jackson, J. B. C. 1997. Reefs since Columbus. *Coral Reef* 16: S23–S32.
- Jeffries, R. L., and J. L. Maron. 1997. The embarrassment of the riches: Atmospheric deposition of nitrogen and community and ecosystem processes. *Trends in Ecology and Evolution* 12: 74–78.
- Kendall, B. E., C. J. Briggs, W. W. Murdoch, P. Turchin, S. P. Ellner, E. McCauley, R. M. Nisbet, and S. N. Wood. 1999. Why do populations cycle? A synthesis of statistical and mechanistic modeling approaches. *Ecology* 80: 1789–1805.
- King, C. M. 1984. *Immigrant Killers: Introduced Predators and the Conservation of Birds in New Zealand*. Auckland: Oxford University Press.
- Kitchell, J. F. (ed.). 1992. *Food Web Management: A Case Study of Lake Mendota*. New York: Springer-Verlag.
- Kitchell, J. F., D. F. Schindler, R. Ogutuohwayo, and P. N. Reintal. 1997. The Nile perch in Lake Victoria—Interactions between predation and fisheries. *Ecological Applications* 7: 653–664.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principles in fisheries management through marine reserves. *Ecological Applications* 8: S72–S78.
- Laws, R. M. 1984. Seals. *Antarctic Ecology* 2: 621–715.
- Leibold, M. A. 1989. Resource edibility and the effect of predators and productivity on the outcome of trophic interactions. *American Naturalist* 134: 922–949.
- Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28: 467–494.
- Letourneau, D. K., and L. A. Dyer. 1998. Experimental test in a lowland tropical forest shows top-down effects through four trophic levels. *Ecology* 79: 1678–1687.
- Lubchenco, J., et al. 1991. The sustainable biosphere initiative: An ecological research agenda. *Ecology* 72: 371–412.
- Ludwig, D., R. Hilborn, and C. J. Walters. 1993. Uncertainty, resources exploitation, and conservation: Lessons from history. *Science* 260: 17, 36.
- May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt, and R. M. Laws. 1979. Management of multispecies fisheries. *Science* 205: 267–277.
- McCann, K. S., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and

- the balance of nature. *Nature* 395: 794–798.
- McCann, K. S., A. Hastings, and D. R. Strong. 1998. Trophic cascades and trophic trickles in pelagic food webs. *Proceedings of the Royal Society of London B* 265: 205–209.
- McCauley, E., W. W. Murdoch, and S. Watson. 1988. Simple models and variation in plankton densities among lakes. *American Naturalist* 132: 383–403.
- McClanahan, T. R., N. A. Muthiga, A. T. Kamukuru, H. Machano, and R. W. Kiambo. 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biological Conservation* 89: 161–182.
- McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. *Science* 266: 1555–1558.
- McNaughton, S. J., M. Oesterheld, D. A. Frank, K. J. Williams. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341: 142–144.
- McQueen, D. J. 1990. Manipulating lake community structure: Where do we go from here? *Freshwater Biology* 23: 613–620.
- McShea, W. J., H. B. Underwood, and J. H. Rappole. 1997. *The Science of Overabundance: Deer Ecology and Population Management*. Washington, D.C.: Smithsonian Institution Press.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: Patterns and importance. *Ecological Monographs* 65: 21–74.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* 285: 1396–1398.
- Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. *Bioscience* 43: 219–224.
- Mittelbach, G. G., C. W. Osenberg, and M. A. Leibold. 1988. Trophic relations and ontogenetic niche shifts in aquatic ecosystems. In B. Ebenman and L. Persson (eds.), *Size-Structured Populations*, pp. 219–233. Berlin: Springer-Verlag.
- Murdoch, W. W. 1966. Community structure, population control, and competition—A critique. *American Naturalist* 100: 219–226.
- Murdoch, W. W., and C. J. Briggs. 1996. Theory for biological control: Recent developments. *Ecology* 77: 2001–2013.
- Murdoch, W. W., J. Chesson, and P. L. Chesson. 1985. Biological control in theory and practice. *American Naturalist* 125: 344–366.
- Murdoch, W. W., R. M. Nisbet, E. McCauley, A. M. deRoos, and W. S. C. Gurney. 1998. Plankton abundance and dynamics across nutrient levels: Tests of hypotheses. *Ecology* 79: 1339–1356.
- Nixon, S. W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia* 41: 199–219.
- NRC (National Research Council). 1994. *Improving the Management of U.S. Marine Fisheries*. Washington, D.C.: National Academic Press.
- Oksanen, L., S. J. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118: 240–261.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14: 483–488.

- Paine, R. T. 1980. Food webs, linkage interaction strength, and community infrastructure. *Journal of Animal Ecology* 49: 667–685.
- Paine, R. T. 1992. Food-web analysis through field measurement of the per capita interaction strength. *Nature* 355: 73–75.
- Parma, A. M., et al. 1998. What can adaptive management do for our fish, forests, food and biodiversity? *Integrative Biology* 1: 16–26.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. Fishing down marine food webs. *Science* 279: 860.
- Persson, L. 1999. Trophic cascades: Abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85: 385–397.
- Persson, L., G. Andersson, S. F. Hamrin, and L. Johansson. 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In S. R. Carpenter (ed.), *Complex Interactions in Lake Ecosystems*, pp. 45–68. New York: Springer-Verlag.
- Persson, L., S. Diehl, L. Johansson, G. Andersson, and S. F. Hamrin. 1992. Trophic interactions in temperate lake ecosystems: A test of food chain theory. *American Naturalist* 140: 59–84.
- Pinnegar, J. K., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M. L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, G. D'Anna, and C. Pipitone. 2000. Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management. *Environmental Conservation* 27: 179–200.
- Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86: 3–15.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28: 289–316.
- Polis, G. A., and S. D. Hurd. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147: 396–423.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147: 813–846.
- Pomeroy, L. R. 1974. The ocean's food webs: A changing paradigm. *Biological Science* 24: 242–244.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250: 811–814.
- Power, M. E. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? *Ecology* 73: 733–746.
- Power, M. E., D. Tilman, J. E. Estes, B. A. Menge, W. L. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *Bioscience* 46: 609–620.
- Roberts, C. M., and N. V. C. Polunin. 1993. Marine reserves: Simple solutions to managing complex fisheries? *Ambio* 22: 363–368.
- Rosenzweig, M. L. 1971. Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Science* 171: 385–387.
- Roughgarden, J., S. D. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466.

- Russ, G. R., and A. C. Alcala. 1996. Marine reserves: Rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* 6: 947–961.
- Sala, E., and M. Zabala. 1996. Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series* 140: 71–81.
- Savidge, J. A. 1987. Extinction of an island avifauna by an introduced snake. *Ecology* 68: 660–668.
- Schindler, D. W. 1974. Eutrophication and recovery in experimental lakes: Implications for lake management. *Science* 184: 897–899.
- Schoener, T. W. 1993. On the relative importance of direct versus indirect effects in ecological communities. In H. Kawanabe, J. E. Cohen, and K. Iwasaki (eds.), *Mutualism and Community Organization: Behavioral, Theoretical, and Food-Web Approaches*, pp. 365–411. New York: Oxford University Press.
- Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: An ecosystem approach to lake restoration. In P. L. Brezonik and J. L. Fox (eds.), *Proceedings of a Symposium on Water Quality Management through Biological Control*, pp. 85–96. Gainesville: University of Florida.
- Shea, K., et al. 1998. Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution* 13: 371–375.
- Shiomoto, A., K. Tadokoro, K. Nagasawa, and Y. Ishida. 1997. Trophic relations in the subarctic North Pacific ecosystem: Possible feeding effect from pink salmon. *Marine Ecology Progress Series* 150: 75–85.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: A review. *Annual Review of Ecology and Systematics* 16: 269–311.
- Soulé, M. E., E. T. Bolger, A. C. Alberts, R. A. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2: 75–92.
- Spiller, D. A., and T. W. Schoener. 1994. Effects of top and intermediate predators in a terrestrial food web. *Ecology* 75: 182–196.
- Strong, D. R. 1992. Are trophic cascades all wet? *Ecology* 73: 747–754.
- Strong, D. R. 1999. Predator control in terrestrial ecosystems: The underground food chain of bush lupine. In H. Olff, V. K. Brown, and R. H. Drent (eds.), *Herbivores: Between Plants and Predators*, pp. 577–602. Oxford, U.K.: Blackwell Science.
- Terborgh, J., J. A. Estes, P. Paquet, K. Ralls, D. Boyd-Heger, B. J. Miller, and R. F. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. In M. E. Soulé and J. Terborgh (eds.), *Continental Conservation*, pp. 39–64. Washington, D.C.: Island Press.
- Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* 57: 189–214.
- Turner, R. E., and N. N. Rabalais. 1994. Coastal eutrophication near the Mississippi River delta. *Nature* 368: 619–621.
- van der Elst, R. P. 1979. A proliferation of small sharks in the shore-based Natal sport fishery. *Environmental Biology of Fish* 4: 349–362.

- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277: 494–499.
- Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation, and ecosystem effects. *Ecological Monographs* 59: 247–265.
- Waage, J. K., and N. J. Mills. 1992. Biological control. In M. J. Crawley (ed.), *Natural Enemies—The Population Biology of Predators, Parasites and Diseases*, pp. 412–430. Oxford: Blackwell Scientific Publications.
- Walters, C. J. 1986. *Adaptive Management of Renewable Resources*. New York: McMillan.
- Walters, C. J., and J. J. Maguire. 1996. Lessons for stock assessment from the northern cod collapse. *Reviews in Fish Biology and Fisheries* 6: 125–137.
- Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: Interaction chains and interaction modifications. *American Naturalist* 141: 71–89.
- Wootton, J. T. 1995. Effects of birds on sea urchins and algae: A lower-intertidal trophic cascade. *Ecoscience* 2: 321–328.
- Wootton, J. T., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Science of the USA* 90: 1384–1387.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69: 508–515.
- Yodzis, P. 1994. Predator-prey theory and management of multispecies fisheries. *Ecological Applications* 4: 51–58.
- Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology* 67: 635–658.
- Yodzis, P. 2000. Diffuse effects in food webs. *Ecology* 81: 261–266.
- Zaitsev, Yu. P. 1992. Recent changes in the trophic structure of the Black Sea. *Fisheries Oceanography* 1: 180–189.
- Zaret, T. M. 1980. *Predation and Freshwater Communities*. New Haven: Yale University Press.
- Zaret, T. M., and R. T. Paine. 1973. Species introduction in a tropical lake. *Science* 182: 449–455.

EXOTIC SPECIES AND CONSERVATION

Research Needs

Carla D'Antonio, Laura A. Meyerson, and Julie Denslow

OVER THE PAST TWO DECADES, EXOTIC INVASIVE SPECIES HAVE become recognized as an important cause of species declines and native habitat degradation (Vitousek et al. 1997; Wilcove et al. 1998). Although exotic species may increase species richness temporarily, over the long term they contribute to species extinction and therefore a decline in biological diversity. For years invasive exotic species were thought to be second only to land-use change in causing species extinctions (e.g., Soulé 1990; D'Antonio and Vitousek 1992), a claim now verified for fish (Miller et al. 1989), plants (D'Antonio and Dudley 1995), and threatened and endangered animal species in the United States (Wilcove et al. 1998). Approximately 60 percent of the species listed under the Endangered Species Act are threatened by invasive species (or fire suppression). Outside of the United States the proportion is estimated to reach 80 percent (Armstrong 1995; Wilcove et al. 1998). Crooks and Soulé (1999) predict that invasive species will soon become the leading cause of ecological degradation because of the increasing extent of disturbed lands, many of which are particularly vulnerable to domination by invasive nonindigenous species.

Exotic species threaten the persistence of native species assemblages because they can be predators, disease vectors, and competitors. They may so alter ecosystem processes that sustaining populations of native species or restoring ecosystem structure and function becomes difficult and expensive

(Vitousek et al. 1997). Although fewer than 20 percent of exotic species negatively affect native species or ecosystems (Simberloff 1981; U.S. Congress 1993; Williamson and Fitter 1996; D'Antonio and Haubensak 1998), this 20 percent can cause persistent changes to native biodiversity and ecosystem functioning. Species with this potential should receive the top priority for conservation and management efforts.

Despite increasing attention from conservationists and researchers, ability to predict establishment success and impact of nonindigenous species remains limited. In this chapter we suggest directions for research into the ecology of exotic species as they affect the conservation of native species and ecosystems. We focus on those issues for which quantitative biological research is needed to illuminate conservation challenges. For convenience, we divide research needs into (1) those addressing the ecology of invasive species, including pathways of introduction and factors affecting invasiveness, rates of spread, and impacts; and (2) those associated with their management, although we recognize the overlap. These research priorities are summarized in Box 4.1.

Factors Influencing Establishment and Spread

Trade and Pathways of Introduction

Humans have been a major vector of nonindigenous species from the beginnings of exploration, trade, and human migrations. Both the hulls and the holds of ships carry terrestrial and marine plants, animals, seeds, and disease between continents. Today, ballast water (the seawater a vessel takes on in one port, for ballast, and discharges upon arrival at another port) is an important source of introductions into marine and estuarine systems, carrying everything from cholera and botulism bacteria to invertebrates and fish. Estimates of the number of species carried in ballast water at any given moment range from 3,000 to 7,000 (Carlton 1999). We know little about invasion potentials and likely impacts of most of the species being transported.

Today, global trade, travel, and human migration have greatly increased rates of exotic introductions to all countries (U.S. Congress 1993; Mack et al. 2000). Although major pathways of introduction are well known, and many countries have established inspection and quarantine operations to monitor these routes for undesirable introductions, potentially dangerous organisms often arrive by previously unappreciated routes. We lack a comprehensive understanding of the many and varied routes through which introductions can occur.

Even when we are aware of potential pathways, we often do not have critical epidemiological information necessary to predict probabilities of establishment, such as the minimum numbers of individuals needed to establish a viable population and conditions promoting establishment and movement

into native ecosystems. For example, numerous insects and plant pathogens have been found in association with wooden packing material, and the potential damage these species may cause to U.S. forests is well recognized (e.g., Wallner 1996). Much more information is needed on factors that affect establishment and spread of such species in order to develop more effective inspection and monitoring strategies. The risk of introduction is inherent in high trade volume, but we need to better evaluate acceptable levels of risk. Purposefully introduced species also have the potential to be directly problematic themselves or to be vectors of disease. Many are currently screened for associated disease organisms (e.g., White and Waterworth 1996), but the effectiveness of current screening and containment needs more research attention. Research on pathogen testing protocols could improve detection methods.

Undesirable exotic species also may be transported *within* a continent, greatly increasing the rate of spread, the exposure of potentially vulnerable ecosystems, and the magnitude of control problems. We need a better understanding of the relationships among pathway characteristics, frequency and abundance of propagule movements, and rates of invasive spread within continents to best direct policy and control strategies.

Predictors of Invasion and Spread

Species Traits and the Environment

Most exotic species do not become established in their new locales, although the small proportion that do become invasive may cause considerable ecological and economic damage. The attempt to identify common characteristics among those taxa that establish and spread on the one hand and among ecosystems vulnerable to invasions on the other has generated considerable debate. What kinds of species are most likely to invade particular types of ecosystems (Williamson and Fitter 1996; Levine and D'Antonio 1999; Lonsdale 1999; Newsome and Noble 1986; Stohlgren et al. 1999; Symstad 2000)? Because extirpation is close to impossible once an invasive has become established, ecologists are seeking better ways to predict which species are likely to become invasive and which ecosystems are most vulnerable to invasion (Ewel et al. 1999). Reliable predictors of invasibility are not yet available, in part because many models include species invading agricultural lands or other highly disturbed landscapes as well as those that invade natural areas (Parker and Reichard 1998). While establishment of many weedy plants is facilitated by disturbance, the process may differ for species that are invasive in native ecosystems (Hobbs and Huenneke 1992; D'Antonio et al. 1999). Likewise, the relative importance of ecosystem characteristics and disturbance in stimulating the establishment of animals is poorly known.

The most reliable determinant of potential invasibility into natural areas is whether a species has been invasive elsewhere. Reichard and Hamilton (1997) found that the best characteristic for predicting invasiveness among woody taxa in North America was whether the species had been reported to be invasive elsewhere. In the absence of a prior history of introductions, invasive potential must be evaluated based on a species' natural history or on the natural history of better-known congeners. However, congeneric species can differ greatly in their invasiveness, suggesting that the predictive capability of current models is not reliable. We need more information on traits correlated with successful establishment and spread and the circumstances under which they are likely to be important, particularly among closely related or ecologically similar species.

The history of intentional introductions of birds and biological control agents has shown that the number of times a species is introduced and the number of individuals per introduction attempt are the best predictors of successful establishment within the region (Newsome and Noble 1986; Hopper and Roush 1993; Crawley 1989; Veltman et al. 1996; Duncan 1997; Green 1997). Such intentional introductions generally have been made into highly modified ecosystems, like agricultural or urban landscapes. We have less information on correlates of success for exotic species entering native ecosystems. Nonetheless, a recent survey found that the rate of propagule arrival was an important determinant for the spread of exotic species into natural areas (Lonsdale 1999). A regular source of propagules greatly increases the likelihood of spread for many reasons. Small populations of colonists are at risk due to Allee effects, genetic bottlenecks, and the high likelihood of stochastic population extirpation (Williamson 1996). In addition to overcoming genetic or breeding problems, a high rate of propagule rain increases the chance of propagules encountering favorable habitats. D'Antonio et al. (in press) suggest that given high propagule supply rates and suitable climate conditions, virtually any ecosystem may be vulnerable to the establishment of exotic species. Research is needed to determine the circumstances under which factors contributing to population or community resistance can be overwhelmed by high rates of propagule arrival.

Although stochastic natural events can be responsible for establishment failure, they can also contribute to the success of an invader. For example, during the 1989–92 drought in England, river flow dropped sufficiently to allow the Asian mitten crab (*Eriocheir sinensis*), which had long been established at the river mouth, to migrate upriver and become established there. Ironically, even beneficial environmental changes, such as reduced pollution, can facilitate invasion by nonindigenous species that are present in low numbers. Populations of the wood-boring gribble (*Limnoria tripunctata*) exploded in the Long Beach–Los Angeles Harbor in the late 1960s because of pollution

reduction, even though the isopod had been present in the harbor prior to the 1900s (Crooks and Soulé 1999 and references therein). Given widespread effects of chemical pollution, climate change, and alteration of nutrient cycles, it is essential that we develop models to anticipate movement of non-native species across the landscape as a consequence of global change. This may be particularly important for disease organisms whose hosts (presumably native species) may be weakened by environmental stresses.

Until recently, low-diversity simple systems were thought to be most vulnerable to biological invasions (Elton 1958; Levine and D'Antonio 1999; Lonsdale 1999; Stohlgren et al. 1999). Recent analyses suggest, however, that invasions are more likely in regions where species diversity is high (Levine and D'Antonio 1999; Stohlgren et al. 1999; Levine 2000; Stadler et al. 2000). These results are contrary to theory, which holds that high species diversity confers resistance to invasion because resources are more fully used (see Levine and D'Antonio 1999 for a review). However, the same environmental conditions that favor diversity of native species (e.g., high resource availability) may also favor exotic species (Stohlgren et al. 1999; Levine and D'Antonio 1999; Levine 2000; Stadler et al. 2000).

As a result, two relatively new hypotheses have emerged: (1) The most diverse communities may in fact be the most vulnerable to invasion, and (2) species losses from diverse communities may lower their resistance to invasion. The correlation between high diversity and high invasibility suggests also that relatively resource-poor ecosystems are at less risk of invasion. Richardson et al. (2000) suggest that in resource-poor environments invasions may be facilitated by mutualisms either between native species and invaders or between previously established and newly arriving invaders. In parts of the tropics, low rates of invasion have been attributed to resource exhaustion and lack of mutualisms, rather than to competition or community resistance (Richardson et al. 2000; Stadler et al. 2000), but experimental evidence in support of these hypotheses is lacking.

The importance of diversity (and species interactions) to invasibility can vary with spatial scale (Levine and D'Antonio 1999; Planty-Tabacchi et al. 1996; Stohlgren et al. 1999; Symstad 2000; Levine 2000; Wiser et al. 1998). For example, Stohlgren et al. (1999) and Levine (2000) found that only at their subplot and plot levels were the most diverse ecosystems resistant to plant invasions. The relationship between neighborhood mechanisms and community patterns relative to invasions rarely has been examined.

Time Lags during Invasion

The detection of a biological invasion may be delayed considerably after the event because the initial population size is small and difficult to detect. In addition, some populations may exhibit an extended lag period before

population growth becomes explosive (Crooks and Soulé 1999; Hobbs and Humphries 1995; Schmitz and Brown 1997; Mack et al. 2000). Despite the apparent commonness of this phenomenon, its causes are not well understood. Among the potential mechanisms contributing to such lags in population growth are slow intrinsic growth rates of the invader, the occurrence of environmental changes promoting more rapid growth rates, the occurrence of genetic changes leading to higher rates of reproduction (Crooks and Soulé 1999), and the continued introduction of new colonists.

For example, the explosive growth of *Melaleuca* into new Florida habitats may have occurred following a genetic mutation allowing broader environmental tolerance (Ewel 1986; Crooks and Soulé 1999). Richardson et al. (2000) suggested that a long lag phase may reflect the absence and subsequent establishment of a necessary symbiont. For example, pines did not become invasive in the southern hemisphere until human activities distributed spores of ectomycorrhizal fungi, which facilitated the naturalization of the pines (Richardson et al. 2000). Because many mutualisms are nonspecific, an invader may benefit from symbionts not found in its native habitat (Richardson et al. 2000). Other cases of seemingly sudden explosive growth can occur when grazing pressure is reduced by removal of herbivores. On Santa Cruz Island in Southern California, fennel (*Foeniculum vulgare*), an introduced European perennial species, was present but not widespread until introduced cattle and feral sheep were removed as part of a conservation effort. Upon removal of the grazers, fennel grew explosively and is now dominant on more than 10 percent of the island (Crooks and Soulé 1999). Despite the enormous potential impacts of introduced disease organisms on native species and ecosystems, we know almost nothing about rates of population increase after introduction or factors influencing apparent lags or the onset of exponential growth. Because control is more likely when populations are small, it is essential that we understand the nature of the lag phase and factors that affect its duration.

Importance of Genetic Diversity to Invasion

Since the classic publications of Baker and others (*Genetics of Colonizing Species*, Baker and Stebbins, 1965), there has been long-standing interest in genetic changes occurring in populations during expansion stages and the importance of genetic diversity to invasion. Several investigators have demonstrated that species with low genetic diversity can become widespread invaders (e.g., Raybould et al. 1991; Stiven and Arnold 1995), while others have found that high genetic diversity occurs in many widespread invaders (e.g., Novak et al. 1993; Demelo and Herbert 1994). More information is needed on the circumstances under which intraspecific genetic diversity pro-

motes or restricts invasion and the relative importance of phenotypic plasticity in allowing widespread invasion in species populations with low genetic variability. Hybridization between invaders and closely related congeners can also accelerate invasion (Vila et al. in press; Daehler and Carino in press).

Impacts of Exotic Species on Native Species, Communities, and Ecosystems

Because exotic species can affect many properties of native populations, communities, and ecosystems, it is difficult to suggest simple and/or comparable measures of impact suitable for use in different ecosystems. Parker et al. (1999) argue that we need a common currency by which to assess species impacts so that investigators can more easily compare their findings and concerns, and species can be more easily prioritized for control. Here we consider effects of exotic species on the likely persistence of native species to be the primary currency of concern. Very few countries recognize ecological pests as species whose movements should be controlled, and species can pass unimpeded into many countries as long as they are not known to be agricultural pests. Quantitative information is badly needed on the potential for ecological damage of many species, particularly those that are being actively traded in the horticultural or pet trade and those that come along as hitchhikers.

Genetic Effects

Invasive, non-native species can affect native species populations through hybridization. Introgression of genes from non-native species can lead to the almost complete loss of the native gene pool. This kind of "genetic swamping" can lead to extinction of a rare species (Levin et al. 1996; Rhymer and Simberloff 1996). Fisheries studies provide a clear example of how this can occur at the subspecific level. Both exogenous and artificially reared Atlantic salmon (*Salmo salar*) have been released for more than a century (Hindar et al. 1991). These releases overwhelmingly have reduced fitness of native populations regardless of whether the introduced salmon were wild or cultured. Salmonid populations are considered to be genetically adapted to their local environments, and hybridization with cultured salmon has disrupted local gene pools (Hindar et al. 1991).

Numerous examples have been documented of this mechanism of loss or change within a native taxon, particularly in animal species (Miller et al. 1989; Rhymer and Simberloff 1996; Vila et al. 2000). Despite published information documenting such impacts, interspecific hybridization or hybridization among subspecies is generally ignored as a serious threat to native species. So-called native species from nonlocal gene pools are commonly used in restoration, revegetation, and landscaping projects. Yet we know little about the

degree to which these represent a genetic threat to the persistence of native genotypes or subspecies in the surrounding landscape or the degree to which local adaptation of native species even occurs or can be disrupted. Knapp and Rice (1996, 1998) found that the two native grasses most commonly planted in restoration projects in California, *Nassella pulchra* and *Elymus glaucus*, show high among-site genetic heterogeneity and local adaptation. They also found that restoration practitioners were likely responsible for the movement of genotypes around the state to locales distant from their place of origin (E. Knapp, personal communication) and caution that seed collection zones may need to be very restricted for some species to avoid genetic contamination (Knapp and Rice 1996).

The extent to which these exotic genotypes will decrease the fitness of local genotypes is not known. In at least one instance (*Phragmites australis* in the eastern United States), the introduction of an exotic genotype has led to a native species becoming more invasive, with potentially undesired impacts on wildlife habitat (Crooks and Soulé 1999; Chambers et al. 1999). In many cases interspecific hybridization has been demonstrated to contribute to the formation of more invasive genotypes, which then replace both native species and the original invader (Thompson 1991; Ayres et al. 1999).

Population, Community, and Ecosystem Impacts

Invasive exotic species can cause the decline of native species directly through competition, predation, or disease, or by altering ecosystem processes such that native species begin to die out. Predicting species impacts depends on understanding how traits of the invading species operate under the circumstances of the recipient ecosystem. Impact quality and quantity are affected by the abundance of the invasive species, its particular traits (e.g., rates of food consumption or resource uptake), and characteristics of species in the invaded community. Very few studies quantify impacts of plant invaders, and no systematic review of species traits and their population or community-level impact has been carried out.

Most extinctions caused by species invasions have been due to the introduction of predators of a size (e.g., Nile perch in Lake Victoria) or a feeding type (e.g., snakes in Guam) with no historical precedence in the invaded ecosystem. Pathogenic organisms also have caused extinctions (e.g., avian malaria in Hawaii), presumably when native species lack appropriate resistance. By contrast, exotic species that merely compete with native species contribute to species declines (e.g., Daehler and Carino 1999) but appear less likely to cause extinctions by themselves (Frankel and Soulé 1981).

Vitousek (1990) suggested a conceptual framework for predicting when the addition or deletion of a species is likely to have an ecosystem impact. He

predicted that species causing ecosystem impacts are those that (1) introduce a new trophic level to the system, (2) alter the rate of resource supply to the system, or (3) alter the disturbance regime. Similarly, Chapin et al. (1996) suggest that species affecting ecosystem processes have traits that are qualitatively different from the native species in the invaded sites. They and others (Mack and D'Antonio 2001) predict that invaders whose traits differ only quantitatively from native species will affect native species largely through competitive interactions. Some effects on ecosystem processes and community structure may take many years to be manifested. Selective comparisons—e.g., of the impacts of an invasive through a range of invaded habitats, or of the impacts of different kinds of invaders—will be particularly useful to elucidate these ideas.

In addition, we have an urgent need to understand how impacts at one trophic level will translate to other levels. Pathogens such as plant diseases and animal viruses can reduce the abundance of their hosts quickly (see chapter 8). If these species interact strongly with other species—e.g., are important sources of food or shelter—their elimination could be catastrophic for entire communities.

While there has been much debate about the relationship between species diversity and community susceptibility to invasion, there has been little discussion of how native diversity moderates the *impacts* of exotic species. On the basis of his observation that introduced species had large impacts on island ecosystems, Elton (1958) suggested that more simple (and therefore presumably less diverse) ecosystems were more likely to be affected strongly by non-native species. Simberloff (1995) and D'Antonio and Dudley (1995) likewise found that extinctions caused by invasive exotic species were more common on island ecosystems originally lacking some functional groups. However, there have been few studies of the relationship between diversity and the impact of invaders in continental ecosystems, particularly where diversity within and among functional groups or trophic levels is manipulated.

If invading species interact with natives primarily through competition for limited resources, removal of the exotic should produce a compensatory increase in native populations if propagule supply is not limited. If so, then impacts of exotics should be reversible in the course of a restoration program. However, if invaders alter ecosystem processes such as disturbance regimes or soil processes, impacts may not be readily reversed. For example, the introduction of fire-enhancing grasses to semi-arid ecosystems has greatly increased fire frequency in many ecosystems (D'Antonio and Vitousek 1992). Grass populations are not controlled easily nor are grass-fire cycles easily interrupted. In addition, the changes caused by the altered disturbance regimes are not easily reversed. More research is needed to determine the

types of impacts that are reversible and the relationship among traits of the invaders, likelihood of control, and reversibility of impacts.

Effects and Invasiveness of Genetically Modified Organisms

Genetically modified organisms (GMOs) are produced by the insertion of genes into or the removal of genes from a target organism to confer more desirable or delete undesirable traits. This technology has been used in place of traditional plant breeding programs, for example, to significantly decrease the development time for commercial varieties of crops or to increase resistance to herbivores (Paoletti and Pimentel 1996). Several ecologists have pointed out that the release of GMOs is analogous to the introduction of exotic species (Levin 1988; Parker and Kareiva 1996). An important question in terms of conservation biology is whether GMOs will invade natural ecosystems, hybridize with related species, and/or in some way threaten native populations and communities (Raybould and Gray 1994; Parker and Kareiva 1996; Beringer 2000; Hails 2000). Concern has also been raised that wild animal populations will be attracted to pollen produced by a genetically modified crop but will be killed by compounds such as insecticides that are produced by the crop (Poppy 2000). There are almost no ecological data to bring to bear on the controversy.

There has been considerable alarm among the public over the introduction of genetically modified organisms, particularly in Europe. While it is generally assumed that most intentional introductions of GMOs will be benign, it is also acknowledged that some risks exist, since novel genotypes will be created and introduced to environments that are new to them (Levin 1988). In the United States, companies that want to commercialize genetically modified crops are required to show that their product will not become more of a pest species than its unaltered counterpart. However, these requirements are not considered to be rigorous enough by some ecologists, since it can be very difficult to anticipate the invasiveness of particular species or genotypes (Purrington and Bergelson 1995) or to anticipate the rate of pollen movement between GMOs and wild relatives. Considerable doubt surrounds the successful prediction of invasiveness based on the examination of DNA sequences, especially because thus far progress has been limited in predicting invasiveness based on factors better understood than DNA, such as character traits (Purrington and Bergelson 1995; Bergelson 1994; but see Rejmanek 1996).

Experimental and observational work to date does suggest that GMO pollen will spread to wild populations (e.g., Timmons et al. 1995; Lefol et al. 1996), but the extent to which this will occur or is a threat to native populations is debated (Salisbury 2000; Wilkinson et al. 2000). The potential "weed-

iness" of GMOs themselves is also controversial. In a set of experiments with *Arabidopsis thaliana*, Bergelson (1994) found that the genetically altered genotypes bred for herbicide resistance produced fewer seeds and thus had reduced fitness relative to wild-type genotypes. They were nonetheless equally as weedy as their wild relatives. She interpreted this outcome as being the result of population size being limited by something other than seed number. A broad conclusion from this work is that field experiments under a variety of conditions are necessary to ascertain the true ecological risks associated with GMOs (Bergelson 1994).

From an ecological point of view, a significant flaw in the testing of GMOs for commercial release has been the failure to determine whether these species will become invasive if they escape to natural areas. Such testing would require experimentation under a range of realistic field conditions, and this is rarely done. In addition, weeds that are already present in a system are equally likely to benefit from the new traits such as herbicide resistance, insect resistance, stress tolerance, and the ability to fix nitrogen. For example, there is the potential introgression of herbicide resistance to closely related species that are already considered "weedy," making management even more difficult (Hails 2000). Further, reciprocal hybrids of crops and wild species must be studied even if they do not exist in the country where the GMO originated, since some countries that receive GMO products may be home to the wild relatives, and many countries may lack sufficient regulations and/or resources for proper screening (Purrington and Bergelson 1995).

While genetically modified crops might have some environmental benefits because they reduce the need for the use of herbicides and pesticides (Beringer 2000), the topic remains highly controversial among ecologists and the public alike. At a minimum, more rigorous experimental testing, as well as limiting use of GMO crops to areas where no wild relatives are found, will help to reduce the risk of genetically engineered plant invaders (Barrett 2000).

Control of Invasive Species and Restoration of Communities and Ecosystems

Limited resources and lack of consensus by land managers, conservationists, and the general public mandate that we develop a better understanding of the biological and economic consequences of prevention, mitigation, and control measures against invasive species. Potential control mechanisms include import restrictions, mechanical and chemical control programs, and the use of other exotic species to reduce target species and restore environments and communities. Ultimately, the allocation of resources for invasive species management and the protocols through which such management is implemented are matters for public debate and resolution. In many cases,

however, we lack both the factual and the theoretical basis with which to inform those discussions. We will need a broad understanding of the consequences of both action and inaction in the application of control protocols on which to base appropriate risk analyses.

Fundamental ecological information is necessary for developing priorities for exotic species removal, control, or use (see above). For example, development of reliable risk analyses will require more extensive research into the combination of species characteristics, community composition, and ecosystem processes that lead to explosive population growth; a better understanding of the impacts invasive species have on community and ecosystem characteristics; and research into the relative roles of propagule availability, resource supply, and community structure in determining establishment rates of both exotic and native species.

Such information will form the necessary foundation on which to develop priorities for exotic species management in natural ecosystems. Many naturalized exotic species may not threaten native species or compromise management goals (Williams 1996). In Hawaii, of more than nine hundred exotic species naturalized in native communities, less than 10 percent are seen as presenting a current threat to native species or ecosystem processes (Wester 1992). However, invasive species may persist at low population levels for many years before explosive population growth brings them to the attention of managers (Crooks and Soulé 1999), yet control is more easily effected while populations and ranges are small.

Even where ecological impacts of invasive species are substantial, their removal or control is likely to be only part of a long-term management program. Reestablishment of native communities is rarely accomplished by elimination of an invasive exotic. Seed stocks may be lost, disturbance regimes may be altered, and high resource availability after the disturbance associated with removal may favor establishment of other exotics. A substantial part of community structure may depend on timing and opportunity for establishment, and biotic structuring forces may be overwhelmed by seed inputs from exotic species. Removal or reduction of a dominant exotic may not reestablish critical ecosystem processes such as disturbance regimes (Adler et al. 1998; Cabin et al. 2000; Mack and D'Antonio 1998), soil chemistry (Macdonald and Richardson 1986; Vivrette and Muller 1977; D'Antonio 1990; Vitousek et al. 1987), and hydrology (Lacey et al. 1989). Experimental studies of the removal or reduction of exotic species would contribute to understanding of their impacts and of processes affecting subsequent community structure and ecosystem processes (Morrison 1997). Priorities for exotic control should include projections of the composition and structure of the post-removal community, yet the consequences of control are poorly

understood and are often not anticipated. Under what circumstances does control or removal of an invasive species reverse its impact or lead to a less desirable condition?

Although exotic species are often introduced intentionally for habitat restoration and invasive species control, our understanding of the risks involved is limited. Cover crops are used as part of large-scale restoration efforts to slow environmental degradation, reduce erosion, improve soil structure and nutrient supply, moderate microclimates, and alter disturbance regimes (NRC 1993; Richardson 1999). Selected species are often exotics, because cultural information on native species may be wanting, seed supply may be insufficient, or native species may not possess the appropriate characteristics for the intended purposes. Although native species may establish under such cover crops (e.g., Parotta 1992; Lugo 1992), exotics also may retard early seedling establishment, persist as a semipermanent component of the landscape, and in some cases become invasive as well. *Leucaena leucocephala*, a nitrogen-fixing legume, was broadcast aurally over Guam and Saipan to control erosion following the devastating World War II bombardment; fifty years later, the northern portion of the island is dominated by this early successional species, and native forests are much restricted in distribution. Moreover, Richardson (1998, and references cited therein) offers evidence that tree species that cause the greatest problems as invasives are those that have been most widely planted for the longest period of time, suggesting that under appropriate circumstances most widely planted trees in alien environments are likely to become problematic.

Predators, herbivores, and pathogens from their native ranges may be introduced as control agents for invasive species. Biological control often offers the only viable option for reducing populations of widespread exotics, for which it provides a low-cost method with relatively low impact on native ecosystems (Odour 1999). Although the risk of adverse impact on nontarget species has been reduced from the early days of biological control, when introductions were accomplished with less research and the value of nontarget indigenous species was less appreciated (Simberloff and Stiling 1996; Howarth 1991), appropriate pre- and post-release research on impacts to native species and communities is relatively recent. The unique combinations of species, environment, and community that characterize any introduction of an exotic species make predicting the consequences difficult. Higher-order interactions (parasite-host interactions, pollination systems, trophic structures) are particularly difficult to predict in advance (Memmott 1999). A better understanding of the consequences of such introductions based on field and lab experiments in habitats of origin and introduction would provide a better basis for assessing risk.

BOX 4.1. Research Priorities for Invasive, Non-Native Species and Their Potential Impacts on Natural Populations and Communities of Ecosystems

Investigate Pathways of Introduction:

- †1. What are the critical pathways of introduction of new species, and how do they differ in contributing harmful nonindigenous species? For example:
 - †• Introduced plant pathogens can have devastating consequences for entire ecosystems. What are the most important pathways for their arrival, and how do they subsequently spread?
 - †• Introduced insects may also strongly affect forested ecosystems and may carry pathogens. What are the most common pathways for harmful nonindigenous insect species to arrive in new locales, and how does the likelihood of their successful establishment scale with volume of trade?
- †*2. What are acceptable levels of risk of entry of known potential invaders, how well do protocols established to prevent accidental introductions really work, and how can protocols be improved?
3. How do minimum viable population sizes of invaders vary among species, ecosystems, and establishment circumstances? Are there useful generalizations to be made here that might help development of monitoring and screening strategies?
- †*4. Under what circumstances do intentional introductions for commercial purposes contribute to the introduction and spread of harmful invasive species? Can we develop reliable risk assessment protocols to screen intentional introductions for potential invaders, particularly harmful ones?

Investigate the Processes of Invasion and Spread

1. What traits characterize species with high potential for rapid spread beyond their site of introduction?
2. What are the characteristics of natural communities that affect their resistance to invasion? How does propagule pressure interact with resistance, and under what circumstances can we expect propagule pressure to overwhelm resistance?
- *3. How will the spread of non-native species be affected by other global changes, such as chemical pollution, climate change, altered disturbance regimes, and alteration of biogeochemical cycles? For example:
 - Will nitrogen deposition increase rates of plant invasions by favoring fast-growing non-native species?
 - Will changes in storm frequencies and intensities affect the persistence of native populations and potentially favor disturbance-loving exotic species?
 - Will increasing environmental stresses such as air- or water-borne pollutants make native species more susceptible to introduced diseases?

- †4. Why are tropical ecosystems less invaded by nonindigenous species than their temperate counterparts? Will increasing fragmentation of tropical habitats and propagule pressure from exotic species alter this pattern?
5. What is the relationship between neighborhood-scale species interactions that affect invader success and landscape-level patterns of invasion and impact?
- *6. Why are there often long time lags between establishment and the explosive growth and spread of introduced populations? Are there commonalities among species in their invasion patterns relative to the occurrence of time lags?
7. How does genetic diversity influence rates or patterns of invasion?
- †8. How do human activities and cultural patterns—e.g., road construction, land-use patterns, traditional uses of plants, and visitation to reserves—affect the introduction and spread of invasive species?

Assess Impacts

- †*1. What is the potential for introgression of introduced genes to native species, and under what circumstances is this likely to cause a change (either positive or negative) in fitness (and hence ecological performance)? How does the likelihood of such introgression vary among mating systems and life history characteristics of introduced taxa?
2. What traits of exotic species increase the danger of genetic threats to native species? What ecosystem characteristics are associated with high rates of genetic introgression?
3. Which species traits (or combinations thereof) are most likely to threaten local persistence of native species or create difficult-to-reverse impacts on ecosystem processes?
4. Does the arrival and establishment of one or a few non-native species influence the establishment of further alien species?
- *5. How can knowledge of species traits be overlain or interfaced with ecosystem traits to predict species impact?
6. What kinds of higher-order effects—e.g., on other trophic levels or on community processes—are associated with interspecific interactions involving introduced species?
7. How do species richness, functional diversity, and trophic complexity influence the impact of an invader?
- *8. Under what circumstances are impacts of an invasive species likely to be reversible? Are ecosystem effects longer lasting or farther reaching than competition or predation effects? Are impacts due to competition or predation more likely to cause population declines or extinction among native species?

(continues)

BOX 4.1. (Continued)**Consider Genetically Modified Organisms**

- †1. Under what circumstances might GMOs or their genes be able to spread beyond points of introduction?
- †2. Under what circumstances might the spread of GMOs or their genes into wildland habitat pose a threat for native species or ecosystem structure and function?
- †3. What criteria are needed to develop protocols for release and risk assessment associated with GMOs?

Study Control, Restoration, and Their Interactions

- †1. How do we develop priorities for exotic species removal, control, or use?
2. Under what circumstances does control or removal of an invasive species lead to a less desirable condition?
3. Under what circumstances is the introduction of exotic species warranted for restoration or for biological control of invasive non-native species?

Note: An asterisk indicates a top research question. A dagger indicates a research priority that needs an answer within next ten years, or it will be too late for many species or natural communities.

Concluding Remarks

Native biological diversity is valued for many reasons. Its preservation is one of the major challenges of this century. Invasive nonindigenous species contribute to this challenge because a small but significant fraction of them interfere with native species and contribute to their demise on a local or even global scale. Some alter ecosystem processes such that there is a complete alteration of community composition, structure, and function. To reduce the risk of introduction and spread of harmful invaders and better manage existing nonindigenous species for the benefit of native biological diversity, we need greater access to basic information on their ecology and the ecology of the potential systems they might enter. In addition, we need greater coordination among agencies and institutions conducting that research and coordinated development of databases that can be made available to managers.

LITERATURE CITED

- Adler, P., C. M. D'Antonio, and J. T. Tunison. 1998. Understory succession following a dieback of *Myrica faya* in Hawaii Volcanoes National Park. *Pacific Science* 52:69–78.
- Armstrong, S. 1995. Rare plant protects Cape's water supplies. *New Scientist* (Feb. 11): 8.
- Ayres, D. R., D. Garcia-Rossi, H. G. Davis, and D. R. Strong. 1999. Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA, determined by random amplified polymorphic DNA (RAPDs). *Molecular Ecology* 8:1179–1186.
- Baker, H. G., and G. L. Stebbins. 1965. *The Genetics of Colonizing Species*. New York: Academic Press.
- Barrett, S. C. H. 2000. Microevolutionary influences of global changes on plant invasions. In *Invasive Species in a Changing World*, edited by H. A. Mooney and R. J. Hobbs, pp. 115–139. Washington, D.C.: Island Press.
- Bergelson, J. 1994. Changes in fecundity do not predict invasiveness: A model study of transgenic plants. *Ecology* 75:249–252.
- Beringer, J. E. 2000. Releasing genetically modified organisms: Will any harm outweigh the advantage? *Journal of Applied Ecology* 37:207–214.
- Cabin, R. J., S. Weller, D. Lorence, T. Flynn, D. A. Sakai, D. Sandquist, and L. Hadway. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. *Conservation Biology* 14:439–453.
- Carlton, J. T. 1999. The scale and ecological consequences of biological invasions in the world's oceans. In *Invasive Species and Biodiversity Management*, edited by O. T. Sandlund, P. J. Schei, and Å. Viken, pp. 195–212. New York: Kluwer Academic Publishers.
- Chambers, R. M., L. A. Meyerson, and K. Saltonstall. 1999. Expansion of *Phragmites australis* into tidal wetlands of North America. *Aquatic Botany* 64:261–273.
- Chapin, F. S. III, H. Reynolds, C. M. D'Antonio, and V. Eckhart. 1996. The functional role of species in terrestrial ecosystems. In *Global Change in Terrestrial Ecosystems*, edited by B. Walker and W. Steffan, pp. 403–430. Cambridge, U.K.: Cambridge University Press.
- Crawley, M. J. 1989. Chance and timing in biological invasions. In *Biological Invasions: A Global Perspective*, edited by J. A. Drake et al., pp. 407–423. New York: John Wiley.
- Crooks, J. A., and M. E. Soulé. 1999. Lag times in population explosions of invasive species: Causes and implications. In *Invasive Species and Biodiversity Management*, edited by O. T. Sandlund, P. J. Schei, and Å. Viken, pp. 103–125. New York: Kluwer Academic Publishers.
- Daehler, C. C., and D. A. Carino. 1999. Threats of invasive plants to the conservation of biodiversity. In *Biodiversity and Allelopathy: From Organisms to Ecosystems in the Pacific*, edited by C. H. Chow et al., pp. 21–27. Taipei: Academia Sinica.

- Dachler, C. C. and D. A. Carino. 2001. Hybridization between native and alien plants and its consequences. In *Biotic Homogenization: The Loss of Biodiversity through Extinction and Invasion*, edited by J. L. Lockwood and M. L. McKinney, pp. 85–106. New York: Kluwer Academic Publishers.
- D'Antonio, C. M. 1990. *Invasion of Coastal Plant Communities by the Introduced Succulent, Carpobrotus edulis (Aizoaceae)*, Ph.D. dissertation, University of California, Santa Barbara.
- D'Antonio, C. M., and Dudley, T. L. 1995. Biological invasions as agents of change on islands versus mainlands. In *Islands: Biological Diversity and Ecosystem Function*, edited by P. M. Vitousek, L. Loope, and H. Adersen, pp. 103–121. Berlin: Springer-Verlag.
- D'Antonio, C. M., T. L. Dudley, and M. C. Mack. 1999. Disturbance and biological invasions: Direct effects and feedbacks. In *Ecosystems of Disturbed Ground*, edited by L. Walker, pp. 413–452. Oxford, U.K.: Elsevier.
- D'Antonio, C. M., and K. A. Haubensak. 1998. Community and ecosystem impacts of introduced species. *Fremontia* 26:13–18.
- D'Antonio, C. M., J. Levine, and M. Thomsen. In press. Ecosystem resistance to invasion and the role of propagule supply: A California perspective. *Journal of Mediterranean Environments* 1.
- D'Antonio, C. M., and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Demelo, R., and P. D. M. Herbert. 1994. Founder effects and geographical variation in the invading cladoceran *Bosmina* (Eubosmina) *coregoni* (Baird 1857) in North America. *Heredity* 73:490–499.
- Duncan, R. P. 1997. The role of competition and introduction effort in the success of passeriform birds introduced into New Zealand. *American Naturalist* 149:903–915.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. London: Methuen.
- Ewel, J. 1986. Invasibility: Lessons from south Florida. In *Ecology of Biological Invasions of North America and Hawai'i*, edited by H. A. Mooney and J. Drake, pp. 214–230. New York: Springer-Verlag.
- Ewel, J. J., D. J. O'Dowd, and 19 others. 1999. Deliberate introductions of species: research needs. *Bioscience* 49:619–630.
- Frankel, O. H., and M. E. Soulé. 1981. *Conservation and Evolution*. New York: Cambridge University Press.
- Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *Journal of Animal Ecology* 66:25–35.
- Hails, R. S. 2000. Genetically modified plants—The debate continues. *Trends in Ecology and Evolution* 15: 14–18.
- Hindar, K., N. Ryman, and F. Utter. 1991. Genetic effects of cultured fish on natural populations. *Canadian Journal of Fisheries and Aquatic Science* 48:945–957.
- Hobbs, R., and L. F. Huenneke. 1992. Disturbance, diversity and invasion: Implications for conservation. *Conservation Biology* 6:324–337.

- Hobbs, R., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9:761–770.
- Hopper, K. R., and R. T. Roush. 1993. Mate finding, dispersal, number released and the success of biological control introductions. *Ecological Entomology* 18: 321–333.
- Howarth, F. G. 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* 36:485–509.
- Knapp, E., and K. J. Rice. 1996. Genetic structure and gene flow in *Elymus glaucus* (blue wildrye): Implications for native grassland restoration. *Restoration Ecology* 4:1–10.
- Knapp, E., and K. J. Rice. 1998. Comparison of isozymes and quantitative traits for evaluating patterns of genetic variation in purple needlegrass (*Nassella pulchra*). *Conservation Biology* 12:1031–1041.
- Lacey, J. R., C. B. Marlow, and J. R. Lane. 1989. Influence of spotted knapweed (*Centaurea maculosa*) on surface runoff and sediment yield. *Weed Technology* 3:627–631.
- Lefol, E., A. Fleury, and H. Darmency. 1996. Gene dispersal from transgenic crops: II. Hybridization between oilseed rape and the wild hoary mustard. *Sexual Plant Reproduction* 9:189–196.
- Levin, D. J., J. Francisco-Ortega, and R. K. Jansen. 1996. Hybridization and the extinction of rare plant species. *Conservation Biology* 10:10–16.
- Levin, S. A. 1988. Safety standards for the environmental release of genetically engineered organisms. *Trends in Ecology and Evolution* 3:S47–S49.
- Levine, J. M. 2000. Species diversity and biological invasions: Relating local process to community pattern. *Science* 288:761–763.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* 87:15–26.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536.
- Lugo, A. E. 1992. Tree plantations for rehabilitating damaged forest lands in the tropics. In *Ecosystem Rehabilitation: Preamble to Sustainable Development, Volume 2*, edited by M. K. Wali, pp. 247–255. The Hague, Netherlands: Academic Press.
- Lugo, A. E. 1988. The future of the forest: Ecosystem rehabilitation in the tropics. *Environment* 30:41–45.
- Macdonald, I. A. W., and D. M. Richardson. 1986. Alien species in terrestrial ecosystems of the fynbos biome. In *The Ecology and Management of Biological Invasions in Southern Africa*, edited by I. A. W. Macdonald et al., pp. 77–91, Cape Town, Republic of South Africa: Oxford University Press.
- Mack, M., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195–198.
- Mack, M., C. M. D'Antonio, and R. Ley. 2001. Pathways through which exotic grasses alter ecosystem nitrogen cycling in seasonally dry Hawaiian woodlands. *Ecological Application*, in press.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, and M. Clout. 2000. Biotic invasions: Causes, epidemiology, global consequences and control. *Ecological*

Applications 10:689–710.

- Memmott, J. 1999. Food webs as a tool for studying nontarget effects in biological control. In *Non-Target Effects of Biocontrol*, edited by P. A. Follett and J. J. Duan, pp. 147–280. New York: Kluwer Academic Publishers.
- Miller, R. R., J. D. Williams, and J. E. Williams. 1989. Extinctions of North American fishes during the past century. *Fisheries* 14: 22–38.
- Morrison, M. L. 1997. Experimental design for plant removal and restoration. In *Assessment and Management of Plant Invasions*, edited by J. O. Luken and J. W. Thieret, pp. 104–117. New York: Springer.
- Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characters of invading species. In *Ecology of Biological Invasions: An Australian Perspective*, edited by R. H. Groves and J. J. Burdon, pp. 1–20. New York: Cambridge University Press.
- Novak, S. J., R. N. Mack, and P. S. Soltis. 1993. Genetic variation in *Bromus tectorum* (Poaceae): Introduction dynamics in North America. *Canadian Journal of Botany* 71:1441–1448.
- NRC (National Research Council). 1993. *Vetiver Grass: A Thin Green Line Against Erosion*. Washington, D.C.: National Academy Press.
- Odour, G. I. 1999. Biological pest control for alien invasive species. In *Invasive Species and Biodiversity Management*, edited by O. T. Sandlund, P. J. Schei, and Å. Viken, pp. 305–321. New York: Kluwer Academic Publishers.
- Paoletti, M. G., and D. Pimentel. 1996. Genetic engineering in agriculture and the environment. *Bioscience* 46:665–673.
- Parker, I. M., and P. Kareiva. 1996. Assessing the risks of invasion for genetically engineered plants: Acceptable evidence and reasonable doubt. *Biological Conservation* 78:193–203.
- Parker, I. M., and S. H. Reichard. 1998. Critical issues in invasion biology for conservation science. In *Conservation Biology for the Coming Decade*, edited by P. L. Fielder and P. M. Kareiva, pp. 283–305. New York: Chapman and Hall.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. Kareiva, M. H. Williamson, B. Von Holle, P. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: Towards a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3–19.
- Parotta, J. A. 1992. The role of plantation forests in rehabilitating degraded tropical ecosystems. *Agricultural Ecosystems and the Environment* 41:115–133.
- Planty-Tabacchi, A., E. Tabacchi, R. J. Naiman, C. DeFerrari, and H. DeCamps. 1996. Invasibility of species rich communities in riparian zones. *Conservation Biology* 10:598–607.
- Poppy, G. 2000. GM crops: Environmental risks and non-target effects. *Trends in Plant Science* 5:5–9.
- Purrington, C. B., and J. Bergelson. 1995. Assessing weediness of transgenic crops: Industry plays plant ecologist. *Trends in Ecology and Evolution* 10:340–342.
- Raybould, A. F., and A. J. Gray. 1994. Will hybrids of genetically modified crops invade natural communities? *Trends in Ecology and Evolution* 9:85–89.
- Raybould, A. F., A. J. Gray, M. J. Lawrence, and D. F. Marshall. 1991. The evolution

- of *Spartina anglica* CE Hubbard (Gramineae): Genetic variation and status of the parental species in Britain. *Biological Journal of the Linnean Society* 44:369–380.
- Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* 11:193–203.
- Rejmanek, M. 1996. What attributes make some plant species more invasive? *Ecology* 77:1655–1661.
- Rhymer, J., and D. Simberloff. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* 27: 83–109.
- Richardson, D. M. 1999. Commercial forestry and agroforestry as sources of alien trees and shrubs. In *Invasive Species and Biodiversity Management*, edited by O. T. Sandlund, P. J. Schei, and Å. Viken, pp. 237–257. New York: Kluwer Academic Publishers.
- Richardson, D. M. 1998. Pines as invaders in the southern hemisphere. In *Ecology Biogeography of Pines*, edited by D. M. Richardson, pp. 450–473. New York: Cambridge University Press.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. Milton, and M. Rejmanek. 2000. Plant invasions—The role of mutualisms. *Biological Reviews* 75:65–93.
- Salisbury, P. A. 2000. The myths of gene transfer: A canola case study. *Plant Protection Quarterly* 15:71–76.
- Schmitz, C., and T. C. Brown. 1997. *Strangers in Paradise*. Washington D.C.: Island Press.
- Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* 49:87–97.
- Simberloff, D. 1981. Community effects of introduced species. In *Biotic Crises in Ecological and Evolutionary Time*, edited by M. H. Nitecki, pp. 53–71. New York: Academic Press.
- Simberloff, D., and P. Stiling. 1996. Risks of species introduced for biological control. *Biological Conservation* 78:185–192.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of non-indigenous species: Invasional meltdown. *Biological Invasions* 1: 21–32.
- Soulé, M. E. 1990. The onslaught of alien species, and other challenges in the coming decades. *Conservation Biology* 4:233–239.
- Stadler, J., A. Trefflich, S. Klotz, and R. Brandl. 2000. Exotic plant species invade diversity hot spots: The alien flora of northwestern Kenya. *Ecography* 23: 169–176.
- Stiven, A. E., and G. L. Arnold. 1995. Phenotypic differentiation among four North Carolina populations of the exotic mussel *Corbicula fluminea* (Muller 1974). *Journal of the Elisha Mitchell Scientific Society* 111:103–115.
- Stohlgren, T., D. Binkley, G. W. Chong, et al. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25–46.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81: 99–109.
- Thompson, J. D. 1991. The biology of an invasive plant. *Bioscience* 41:393–401.
- Timmons, A. M., E. T. O'Brien, Y. M. Charters, S. J. Dubbels, and M. J. Wilkinson. 1995. Assessing the risks of wind pollination from fields of genetically modified

- Brassica napus* spp. *oleifera*. *Euphytica* 85:417–423.
- U.S. Congress, OTA (Office of Technology Assessment). 1993. *Harmful Non-Indigenous Species in the United States*. Washington, D.C.: U.S. Govt. Printing Office.
- Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. *American Naturalist* 147:542–557.
- Vila, M., E. Weber, and C.M. D'Antonio. 2000. Conservation implications of invasion by plant hybridization. *Biological Invasions* 2:207–217.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7013.
- Vitousek, P., C. D'Antonio, L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* 21:1–16.
- Vitousek, P. M., L. Walker, L. Whiteaker, D. Mueller-Dombois, and P. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802–804.
- Vivrette, N. J., and C. H. Muller. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecological Monographs* 47:301–318.
- Wallner, W. E. 1996. Invasive pests (“biological pollutants”) and US forests: Whose problem, who pays? *OEPP/EPPO Bulletin* 26:167–180.
- Wester, L. 1992. Origin and distribution of adventive alien flowering plants in Hawaii. In *Alien Plant Invasions in Native Ecosystems of Hawai'i*, edited by C. P. Stone, C. W. Smith, and J. T. Tunison, pp. 99–155. Honolulu: University of Hawaii Cooperative National Park Resources Study Unit.
- White, G. A. and H. E. Waterworth. 1996. International exchange of horticultural crop germplasm. *HortScience* 31:315–321.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48:607–617.
- Wilkinson, M. J., I. J. Davenport, Y. M. Charters, A. E. Jones, J. Allainguillaume, H. T. Butler, D. C. Mason, and A. F. Raybould. 2000. A direct regional scale estimate of transgene movement from genetically modified oilseed rape to its wild progenitors. *Molecular Ecology* 9:983–991.
- Williams, C. E. 1996. Potential valuable ecological functions of non-indigenous plants. In *Assessment and Management of Plant Invasions*, edited by J. O. Luken and J. W. Thieret, pp. 26–36. New York: Springer.
- Williamson, M. 1996. *Biological Invasions*. London: Chapman and Hall.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. *Ecology* 77: 1661–1666.
- Wiser, S. K., R. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79:2071–2081.
- Zedler, P. H., and G. A. Scheid. 1988. Invasion of *Carpobrotus edulis* and *Salix lasiolepis* after fire in a coastal chaparral site in Santa Barbara County, California. *Madroño* 35: 196–201.

HABITAT FRAGMENTATION

Consequences, Management, and Future Research Priorities

Kendi F. Davies, Claude Gascon, and Chris R. Margules

Change in land use and land cover, and the associated fragmentation of habitat, is one of the most pervasive effects of human activities on the face of the globe. Habitat destruction and fragmentation are the likely primary causes of the increase in the rate of extinction over recent decades (Henle et al. 1996). All measures of habitat destruction and fragmentation in all areas on earth today indicate a severe and accelerating problem (e.g., Whitmore 1997). Even large wilderness areas like the Amazon are becoming fragmented. In the Amazon, forest clearing increased exponentially during the 1970s and 1980s (Fearnside 1987) and continues at an alarming rate. This is significant because the tropics are highly diverse and relatively unknown. In Peninsular Malaysia, for example, there are over three thousand tree species of over 30 cm diameter, compared to fifty species indigenous to continental Europe north of the Alps and west of the Urals (Whitmore 1997).

Many temperate regions are already severely fragmented. The western Australian wheatbelt retains just 7 percent of the original woodland, heath, shrubland, and mallee as fragments spread throughout the landscape (Hobbs 1998). The wheatbelt roughly corresponds with the southwest botanical province of western Australia, an area of 300,000 square kilometers that is a recognized hot spot for floristic biodiversity, with about eight thousand species and 75 percent endemism (Myers et al. 2000; Hobbs 1998; Groombridge 1992).

Habitat fragmentation interrupts all ecological patterns and processes, from ecosystem functions and species interactions (Saunders et al. 1991; Kapos 1989) through species behavior and dispersal patterns (Hanski et al. 1995; Redpath 1995) to the genetic makeup of populations (Oostermeijer et al. 1996; Sarre 1995). The science of ecology is only beginning to come to terms with the impacts of this wide array of phenomena on the persistence or extinction of species. This review is an attempt to summarize what we do know and discuss the implications of that knowledge for the management of fragmented landscapes, and to identify the most pressing needs for future research in habitat fragmentation.

Consequences of Habitat Fragmentation

In this section we present the known effects of fragmentation, first on processes operating at the within-fragment spatial scale, and second on processes operating at the between-fragment spatial scale. Then we extend our discussion by recognizing that fragmented landscapes are dynamic and these known effects are not one-time events. On the contrary, they may be the start of changes that continue over longer time scales and have more far-reaching consequences than is first apparent. In the last part of this section we note that habitat remnants are all different and therefore contribute differentially to regional biodiversity goals.

Processes Operating at the Within-Fragment Scale

Isolation

Fragmentation can increase the risk of local extinction because remnant populations within fragments may be smaller and more isolated than they were in the unfragmented landscape. The factors that contribute to the extinction risk of small populations are: (1) environmental stochasticity, particularly the effect of extreme events or disturbance (e.g., drought, fire); and (2) deterministic threats (e.g., habitat degradation). Two other often-cited effects are probably of less importance but may help to "finish off" a declining population. These are: (3) demographic stochasticity, which affects only very small populations; and (4) loss of genetic variation, which acts relatively slowly in all but the smallest populations (Harrison and Taylor 1997).

Size and Edge Effects

Mounting empirical evidence suggests that habitat modification (a deterministic threat) may be one of the most significant consequences of habitat fragmentation for the persistence of species. Habitat is modified as a result of changes in physical conditions including fluxes of wind, water, solar radiation, fire, and disturbance (Saunders et al. 1991). This in turn can cause

changes to vegetation structure (Laurance et al., *Effects*, 1998; Malcolm 1994), microclimate (Kapos 1989), and ground cover (Didham et al. 1998). However, not all species are affected by a given change in the same way. Often a change that negatively affects one species benefits another (e.g., Davies et al. 2000; Didham et al. 1998; Gascon 1993).

These physical changes to habitat are usually greatest at fragment edges, particularly in forests (e.g., Laurance et al., *Rain Forest*, 1998; Murcia 1995; Malcolm 1994). For example, the large-scale tropical forest fragmentation experiment at Manaus in Brazil recorded an overall reduction in forest biomass, a reduction of the overstory vegetation, and an increase in the understory vegetation of fragments (Laurance et al., *Effects*, 1998; Laurance et al. 1997; Malcolm 1994). Fragment edges were hotter, drier, and windier (Kapos et al. 1997; Kapos 1989), resulting in higher tree mortality at edges (Laurance et al., *Effects*, 1998, Ferreira and Laurance 1997) and increased rates of leaf fall near recent edges (Gascon and Lovejoy 1998; Lovejoy et al. 1986). Air temperature, litter biomass and moisture, and percentage ground cover of twigs were all correlated with distance from edges (Didham et al. 1998). In a similar large-scale forest fragmentation experiment in temperate eucalypt forest at Wog Wog in southeastern Australia, significantly higher counts of fallen logs were recorded near fragment edges, and higher levels of solar radiation were found to be reaching the forest floor. In addition, litter depth and percentage ground cover of leaves and grass were lower in fragments, while cover of bare ground and bark were higher in fragments than in continuous forest (Davies, unpublished data).

Changes in animal distribution follow these edge-induced physical changes to fragments. For example, in fragments of coastal scrub in Southern California, water runoff from surrounding developed areas and reductions in the cover of native vegetation near edges have both facilitated the invasion of the exotic Argentine ant. All three changes have significantly reduced the richness of the native ant fauna, particularly near edges (Saurez et al. 1998). At Manaus in Brazil, beetle species composition changed with both decreasing distance from fragment edges and decreasing fragment area. Environmental variables that changed with distance from fragment edges helped to explain the change in species composition. These variables included canopy height, air temperature, litter biomass, percentage ground cover of twigs, and the moisture content of litter (Didham et al. 1998). At Wog Wog, beetle species composition at small fragment edges was most different post-fragmentation from beetle composition in continuous forest, while beetle species composition at large fragment interiors was not different from that of continuous forest (Davies et al. 2001). These changes in composition were not related directly to the recorded physical changes to fragments, but changes in

the abundance of some individual species were (Davies, unpublished data). Many other studies have hypothesized that physical changes to fragments at least partly explain species responses to fragmentation (e.g., Margules et al. 1994; Stouffer and Bierregaard 1995).

An important point that has been recognized about edge effects is that the edge effect at a site within a fragment is the sum of the influences from all points on all edges (Malcolm 1994; Laurance and Yensen 1991). This means that the size and shape of a fragment are important because, in fragments with large perimeter-to-area ratios, edge effects penetrate a larger proportion of the fragment. However, given a deeply penetrating edge effect, even very large fragments can be entirely physically modified by edge effects. It also means that populations on small fragments can be at risk, not only because populations become small but also because they are subjected to more significant habitat modification. This makes management challenging, because the effects of habitat modification through edge effects are landscape specific, and guidelines must be developed for each situation. In contrast, a metapopulation model of the landscape that focuses on isolation and dispersal allows general guidelines to be developed, but if habitat modification is important, such guidelines may be inappropriate.

Processes Operating at the Between-Fragment Scale

Dispersal

Processes operating at the between-patch scale also affect the persistence of species. The core concept of both metapopulation theory (Levins 1969) and the equilibrium theory of island biogeography (MacArthur and Wilson 1967) is that within-patch dynamics are influenced not only by local extinction but also by colonization from elsewhere in the landscape. As the landscape becomes more fragmented, colonization rates are reduced. As a result, the number of species within a patch declines (MacArthur and Wilson 1967), and extinction risk at the scale of the entire landscape or metapopulation increases (Hanski 1994; Levins 1969).

The focus on metapopulation theory in fragmentation studies has centered conservation ecologists' attention on the importance of dispersal and between-patch dynamics for persistence. However, although theoretical models demonstrate the importance of dispersal, empirical evidence from real landscapes suggests that local dynamics are at least as important over the short term. In a recent review of fragmentation studies, Harrison and Bruna (1999) concluded that the role of spatial dynamics in determining species responses to fragmentation might have been overemphasized. The studies reviewed suggest that local processes, like edge effects and physical changes,

are the main cause of changes to the distribution and abundance of organisms in fragmented landscapes.

However, we must bear in mind that the effects of local processes may have been documented more often simply because those effects are easier to detect than are extinction, colonization, and dispersal dynamics. In addition, it is likely that local processes are important in the short term, but over longer time scales spatial dynamics play a greater role. Many of the studies in real landscapes have documented the effects of fragmentation on particular plant or animal species over only a few generations since fragmentation, whereas the role of spatial dynamics might come into play on time scales of many generations.

Few studies have tried to separate these two classes of mechanism: the importance of local deterministic changes like edge effects and the importance of spatial population dynamics. To address this issue, we need to ask: what kinds of species in what kinds of landscapes lead to important effects of spatial dynamics? An important consideration here is the correspondence between the spatial scale of a local population and the scale at which the landscape is fragmented. We use the term *local population* to refer to the spatial scale over which individuals are well mixed such that individuals can be considered to share the same location, and we use the term *metapopulation* to refer to a collection of local populations (Hanski and Simberloff 1997). At one extreme, the scale of a local population is larger than a single fragment. Thus, individual fragments support parts of a local population but not an entire local population (i.e., a "patchy population," Harrison 1991; e.g., Diffendorfer et al. 1995; Andreassen et al. 1998; Andreassen and Ims 1998). An intermediate match of scales is where one fragment supports a well-mixed local population, and persistence at the landscape scale depends on dispersal among fragments. This is the scale at which metapopulation theory is most often applied to fragmented landscapes (e.g., Hanski 1994; Hanski et al. 1995). At the other extreme, if the scale of a local population is smaller than a fragment, then fragments may be internally patchy, supporting many populations (a metapopulation within fragments). Then, recolonization from within fragments increases persistence at both fragment and landscape scales, even when between-fragment dispersal is low (Holt 1992).

The Matrix

A feature that distinguishes fragmented landscapes from simple island-sea models is that the suitability of the matrix of disturbed or converted lands, in which habitat fragments are embedded, varies among species. The matrix, therefore, has a strong influence on between-patch processes (Holt and Gaines 1993) and has at least four potential roles:

1. The matrix can alter dispersal and colonization rates, which may be reduced or enhanced. Movement through the matrix is more likely when the vegetation structure of the matrix is similar to the fragments (e.g., Stouffer and Bierregaard 1995; Pearson 1993).
2. The matrix can provide alternative habitat for the original species (e.g., Whitmore 1997; Foster and Gaines 1992) and generalist species in particular (Harrison and Bruna 1999; Holt 1997).

Putting roles 1 and 2 together, empirical evidence shows that those species that use matrix habitat surrounding fragments for dispersal or as additional habitat are less vulnerable in fragmented landscapes than those restricted to remnants of wildlands. Gascon et al. (1999) found those species of birds, small mammals, and frogs that were able to tolerate or exploit the matrix were less vulnerable to fragmentation, while species that avoided the matrix tended to decline or disappear. Davies et al. (2000) also found that the group of beetle species that were never detected in the matrix declined in abundance in fragments relative to continuous forest controls, while the group of species that was abundant in matrix habitat increased in abundance in fragments.

3. The matrix may provide suitable habitat for exotic (non-native) species and therefore act as a source of species invading habitat fragments (Gascon et al. 1999; Saurez et al. 1998; Whitmore 1997; Fahrig and Merriam 1994; Halme and Niemelä 1993). Invasions by exotics have frequently been implicated as the cause of ecological change in fragments. There are many examples of highly competitive weed species displacing the original vegetation (e.g., Viana et al. 1997; McIntyre and Laval 1994; Parsons 1972) and of generalist predators causing declines in birds and mammals (reviewed in Tewksbury et al. 1998; Bolger et al. 1997; Soulé et al. 1988).
4. The matrix vegetation type and its structure can determine the severity of edge effects. For example, Amazon rain forest fragments surrounded by pasture had higher tree mortality rates near edges than those surrounded by regrowth forest, and this edge effect penetrated farther in those fragments surrounded by pasture (Mesquita et al. 1999).

Fragmented Landscapes Are Dynamic

To summarize this discussion of consequences so far, we now recognize that fragments are not simply cutout pieces of the original continuous habitat. Physical conditions within fragments are likely to have been altered. We know that for many species, these local alterations may be as important in

determining persistence in fragmented landscapes as are processes operating at the between-patch scale, such as dispersal, at least in the short term. However, it is time we recognized that fragmented landscapes are dynamic and that habitat and physical conditions in fragments are likely to change over time scales longer than the initial fragmentation process (Soulé et al. 1988). We have identified three classes of mechanism that can cause fragments to change in time: loops of positive feedback, cumulative impacts, and cascades of events.

Mechanisms

POSITIVE FEEDBACK LOOPS

Feedback loops place fragments at risk of becoming significantly altered or vanishing altogether. For example, in the Amazon rain forests of Brazil, fragments are embedded in a matrix of sugar cane and eucalyptus plantations. Fire, which is used for management in the matrix, is becoming an important element in the dynamics of these landscapes. Fires encroaching into rain forest fragments create a positive feedback loop (Cochrane et al. 1999). Low-intensity fires kill most contacted rain forest trees because of their characteristically thin bark. This increases the fuel load on the forest floor, which in turn dries out because the canopy becomes more open. Thus, after an initial low-intensity fire, fragments become more susceptible to new fires. In this way, primary forest is readily replaced by secondary species that are in turn eliminated and replaced by exotics that are resistant to fire (Laurance et al., *Effects*, 1998; Viana et al. 1997). In addition, edges can act as a conduit to carry fire into the margins of the primary forest, because invading grasses and weedy vines add highly combustible live fuels to the already high fuel loads (Cochrane et al. 1999). The increasing incidence of fire in this landscape may be sufficient to cause degeneration of forest at fragment edges, leading to receding edges of primary rain forest and the potential for fragments to vanish altogether (Gascon et al. 2000).

In another example, in the wheatbelt of western Australian, the water table is rising because of widespread clearing of the native woodland, heath, shrubland, and mallee for planting to wheat (Hobbs 1993). This region has one of the highest levels of endemism in the world, but this diversity now persists in remnants scattered across the agricultural landscape. The rising water table causes waterlogging but also brings with it salt stored at depth, causing salinization at the soil surface. Even given the best intentions of conservation managers, the rising water table ultimately threatens those remnants in the lower parts of the landscape (Hobbs 1993). As the vegetation on those remnants is killed, the water table may rise even further, threatening, in turn, a

new set of remnants. Without active tree planting in key parts of the landscape, the unique flora and fauna of this region is at great risk.

CUMULATIVE IMPACTS

A cumulative impact can degrade a fragment over time. In the western Australian wheatbelt, the addition of fertilizer in combination with physical disturbance (from sheep grazing) increases both the rate of establishment and the growth of weed species at the edges of remnants (Hobbs and Atkins 1988). The woodland soils are naturally nutrient poor, but fertilizer is applied to wheat crops and nutrient is readily transferred across remnant edges by wind and by defecating livestock (Hobbs 1993; Scougall et al. 1993). Thus, the cumulative addition of nutrients may result in increasingly severe weed invasion, reducing the recruitment of native species (Hobbs 1991) and resulting in the gradual degradation of woodland fragments. In southeastern Australia, the buildup of nutrients in woodland fragments has led to increases in the abundance of defoliating insects, which can eventually kill trees, resulting in the gradual degradation and loss of woodland fragments in those agricultural landscapes (Yates and Hobbs 1997; Landsberg et al. 1990).

CASCADES OF EVENTS

Some of the clearest examples of cascades of events due to fragmentation are trophic cascades (see chapter 3). In a trophic cascade, changes in the presence or abundance of a species at one trophic level in turn affect species at other trophic levels (Carpenter et al. 1985). For example, in coastal Southern California, sage-scrub habitat remains in steep-sided canyons embedded in an urban matrix. The decline and disappearance of the top predator, the coyote, from smaller habitat fragments have resulted in elevated numbers and activity of mesopredators that exert stronger predation pressure on native bird species. As a result, those fragments with coyotes have retained more bird species (Crooks and Soulé 1999).

Trophic cascades can also occur when a species is added to a fragmented landscape or increases in abundance. For example, in the midwestern United States, nest predation and parasitism by cowbirds is greater in forest landscapes that have been more severely fragmented. This has affected the reproductive rates of some neotropical migrant birds so severely that their populations have become sinks, dependent on immigration from populations in landscapes with more extensive forest cover (Robinson et al. 1995).

Another example in which fragmentation has resulted in changes to ecological relationships among species is the reduced rates of pollination observed in fragments of dry Chaco forest in Argentina (Aizen and

Feinsinger 1994) and of rain forest in Manaus (Powell and Powell 1987). Over time, the altered pollination regime could have a cascading effect that leads to the loss of plant species and in turn to their associated biota. Since many tree species live for centuries, we might not see such cascading effects for some time (Whitmore 1997).

Apart from trophic cascades, there is also potential for cascades to be set off when biophysical processes are altered. For example, in the wheatbelt of western Australia, there is evidence that the extent of land clearing and the resulting change in albedo has changed the rainfall pattern: there is now less rain over areas dominated by the agricultural matrix and more rain over areas that are still largely covered by native vegetation (Hobbs 1998). With reduced annual rainfall in remnants, it is easy to imagine that recruitment of some plant species may decline, eventually resulting in the loss of those species. In turn, animals that rely on them as food sources (e.g., herbivores, frugivores, seed eaters) may be threatened, and so on.

There are now many other examples in which ecological function has been impaired by fragmentation. It is easy to imagine that these losses of function could set off cascades of events in time. For example, Klein (1989) showed that fragmentation reduced numbers of dung beetles, resulting in slower decomposition rates of organic matter in small fragments compared to continuous forest. Accumulating organic matter on the forest floor could have cascading effects that place those fragments on a trajectory of change. For example, fires may become more severe from the increased fuel load, resulting in higher tree mortality and loss of species dependent on trees.

Representativeness and Complementarity

As a final point, we recognize that original continuous habitat is always spatially heterogeneous, as plant and animal communities turn over in the landscape in response to environmental gradients or patchiness. This means that within a fragmented landscape, the biota of remnants will be different from one another to some extent, not just miniature versions of a previous continuous habitat (Laurance et al. 1999). Thus, each habitat remnant will contribute different species to make up the full complement of species of the fragmented landscape under consideration (Brooker and Margules 1996). The same principle applies more generally to biodiversity attributes, such as genetic or ecosystem diversity. The contribution of remnants should be measured and priorities then set for protection and the allocation of scarce management resources, according to the magnitude of that contribution (Margules and Nicholls 1987; see also, e.g., Margules 1999; Pressey et al. 1993).

BOX 5.1. Research Priorities on Habitat Fragmentation

Investigate Within-Fragment Effects

- *1. What is the relative importance, for the local persistence of species in fragments, of threats due to fragment size caused by either habitat modification (edge effects and other deterministic threats) or small population size (i.e., local extinction due to environmental and demographic stochasticity, genetic deterioration)?
2. How does the relative importance of these threats (habitat modification versus small population size) vary given:
 - the type of ecosystem (e.g., forest, grasslands)?
 - the type of matrix (e.g., is the structure of the matrix similar to or different from that of the fragments)?
 - the degree of fragmentation (e.g., does one or the other play a greater role in landscapes that are highly fragmented)?
 - the size of a fragment relative to the spatial scale of a local, focal species population?
 - time since fragmentation?
3. In cases where both habitat modification and small population size affect persistence, are their effects additive or multiplicative (synergistic)? Does this depend on the items listed above?

Investigate Between-Fragment Effects

- *1. What is the relative importance of either within-fragment effects (habitat modification and small population size) or between-fragment effects (dispersal) in determining species persistence over the short term (a couple of generations) and over the long term (many generations)?
2. How does the importance of within-fragment effects and between-fragment effects differ in different types of organisms (with respect to traits such as trophic group, rarity, dispersal strategy, habitat specialization) and in different types of landscapes?
3. How important are metapopulation dynamics in populations that have been anthropogenically fragmented?
4. Are metapopulation dynamics more important for species persistence in fragmented landscapes, in landscapes that have been fragmented for long periods?
- *5. How important in determining species persistence in fragmented landscapes is the match of the spatial scale at which populations of a given species are structured and the spatial scale at which the landscape is fragmented?
6. To understand how populations of a given species are structured, we need to know the scale of a local population and the scale of dispersal. To answer 5, we need to study this for many species in many different types of landscapes.

7. How general is the finding that species that can persist in the matrix habitat are more likely to persist, or even increase in abundance, on fragments? (As far as we are aware, this has been found only for forest.)
- *8. Do those species that can persist in the matrix persist or increase in abundance on fragments at the detriment of other species, through interactions?
9. If yes, how important (strong) are those interactions, and does it depend on the type of landscape and/or how similar the matrix habitat is in structure to the fragment habitat?
10. In which landscapes does the matrix facilitate invasions into fragments: When the matrix habitat is similar or different from fragment habitat? When the matrix is intensively managed or not?

Investigate the Dynamics of Species Loss

- *1. Are there dynamic processes that are causing loss of biodiversity (i.e., positive feedback loops, cumulative impacts, cascades)?
- *2. Can we learn anything from synthesizing the findings of existing studies that describe dynamics in fragmented landscapes? Are fragments more likely to deteriorate in particular types of landscapes? Does it depend on the harshness of the matrix, on how intensively the matrix is managed?
3. Are there useful landscape-level indicators for detecting the sustainability or deterioration of fragments within landscapes (e.g., persistence of a range of successional stages or vegetation classes, degree of connectivity)?
4. In particular, determine whether any of these landscape-level indicators have a relationship with trends in populations of individual species in the landscape. If so, for which types of species (what traits do they have in common)? And which, if any, indicator is most effective in which types of landscapes?

Investigate Landscape-Level Strategies

1. What is the best method for making the tradeoff between, on the one hand, preserving important components of biodiversity represented only in small fragments that will need to be intensively managed to prevent them from deteriorating, and, on the other hand, investing scarce management resources in large fragments that may not be representative of regional biotas but are more secure?
2. Where managing small fragments is considered cost effective, what are the best management options?
 - Should we make them larger, or surround them by a buffer zone, and if the latter, what should the physical characteristics of the buffer zone be?
 - How does the particular landscape affect strategies?

Note: Asterisks denote the highest priorities for the current decade.

Research Priorities for the Conservation of Biodiversity

In a research program designed to promote the conservation of biodiversity in fragmented landscapes, we need to develop an understanding of within-fragment, or local, effects because they seem to manifest first. However, understanding those effects is not necessarily of general interest to ecologists because that knowledge may not contribute to general ecological principles. Rather, those effects tend to be system specific and require research that increases local knowledge of natural history. For example, in woodland remnants in the western Australian wheatbelt, there is little or no regeneration of the dominant tree species, *Eucalyptus salmonophloia*. Only detailed experiments are helping to determine which factors, of many candidates, are responsible (e.g., soil compaction from livestock grazing, competition with weeds) (Yates et al. 2000). However, this knowledge probably will not help to build generalizations that are transferable to other systems. Nonetheless, this type of research is critical. In box 5.1 we have tended to emphasize research priorities that build general principles because it is not possible to prescribe system-specific research. However, system-specific research is also essential.

How Should We Proceed?

We advocate the use of well-designed field experiments. We also encourage the intelligent use of natural experiments and comparative studies to increase their explanatory power and extend their inference to greater temporal and spatial scales than are approachable through experimental methods. To date, experiments have provided us with the clearest answers, but their spatial and temporal scales can be limited.

It is important to be able to approach the unplanned or natural "experiments" in such a way that clear conclusions can be drawn. In unplanned fragmented landscapes, the opportunities to incorporate key elements of experimental design, such as controls and prefragmentation data, are usually limited. Then, the way forward is through a combination of observation and fitting of specific models (Steinberg and Kareiva 1997). Thus, perhaps the most important issue for studies in unplanned fragmented landscapes is the formulation of adequate models, which should consider effects of the matrix, population structure within and between fragments, and habitat modification.

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LITERATURE CITED

- Aizen, M.A., and P. Feinsinger. 1994. Forest fragmentation, pollination and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75: 330–351.
- Andreassen, H.P., K. Hertzberg, and R.A. Ims. 1998. Space use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. *Ecology* 79: 1223–1235.
- Andreassen, H.P., and R. A. Ims. 1998. The effects of experimental habitat destruction and patch isolation on space use and fitness parameters in female root vole *Microtus oeconomus*. *Journal of Animal Ecology* 67: 941–952.
- Bolger, D.T., A.C. Alberts, R.M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M.E. Soulé. 1997. Response of rodents to habitat fragmentation in coastal Southern California. *Ecological Applications* 7: 552–563.
- Brooker, M.G., and C.R. Margules. 1996. The relative conservation value of remnant patches of native vegetation in the wheatbelt of western Australia: I. Plant diversity. *Pacific Conservation Biology* 2: 268–278.
- Carpenter, S.R., J.F. Kitchell, and J.R. Hogson. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35: 634–639.
- Cochrane, M.A., A. Alencar, M.D. Schulze, C.M. Souza, D.C. Nepstad, P. Lefebvre, and E.A. Davidson. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* 284: 1832–1835.
- Crooks, K.R., and M.E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Science* 400: 563–566.
- Davies, K.F., and C.R. Margules. 1998. Effects of habitat fragmentation on carabid beetles: Experimental evidence. *Journal of Animal Ecology* 67: 460–471.
- Davies, K.F., C.R. Margules, and J.F. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* 81: 1450–1461.
- Davies, K.F., B.A. Melbourne, and C.R. Margules. 2001. Effects of within and between-patch processes on beetle-community dynamics in experimentally fragmented forest. *Ecology*: in press.
- Didham, R.K., P.M. Hammond, J.H. Lawton, P. Eggleton, and N.E. Stork. 1998. Beetle species responses to tropical forest fragmentation. *Ecological Monographs* 68: 295–323.
- Diffendorfer, J.E., M.S. Gaines, and R.D. Holt. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology* 76: 827–839.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. *Conservation Biology* 8: 50–59.
- Fearnside, P.M. 1987. Deforestation and international economic development projects in Brazilian Amazon. *Conservation Biology* 1: 214.
- Ferreira, L.V., and W.F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. *Conservation Biology* 11: 797–801.
- Foster, J., and M.S. Gaines. 1992. The effects of a successional habitat mosaic on a small mammal community. *Ecology* 72: 1358–1373.
- Gascon, C. 1993. Breeding-habitat use by five Amazonian frogs at forest edges. *Biodiversity and Conservation* 2: 438–444.

- Gascon, C., and T.E. Lovejoy. 1998. Ecological impacts of forest fragmentation in central Amazonia. *Zoology, Analysis of Complex Systems* 101: 273–280.
- Gascon, C., T.E. Lovejoy, R.O.J. Bierregaard, J.R. Malcolm, P.C. Stouffer, H. Vasconcelos, W.F. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species persistence in tropical forest remnants. *Biological Conservation* 91: 223–229.
- Gascon, C., G.B. Williamson, and G.A.B. da Fonseca. 2000. Receding forest edges and vanishing reserves. *Science* 288: 1356–1358.
- Groombridge, B. 1992. *Global Biodiversity Status of the Earth's Living Resources*. London: Chapman and Hall.
- Halme, E., and J. Niemelä. 1993. Carabid beetles in fragments of coniferous forest. *Annales Zoologica Fennici* 30: 17–30.
- Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution* 9: 131–135.
- Hanski, I., T. Pakkala, M. Kuussaari, and G. Lei. 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos* 72: 21–28.
- Hanski, I.A., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. In *Metapopulation Biology: Ecology, Genetics and Evolution*, eds. I. A. Hanski and M. E. Gilpin, pp. 5–26. San Diego: Academic Press.
- Harrison, S. 1991. Local extinction in a metapopulation context: An empirical evaluation. *Biological Journal of the Linnean Society* 42: 73–88.
- Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: What do we know for sure? *Ecography* 22: 225–232.
- Harrison, S., and A.D. Taylor. 1997. Empirical evidence for metapopulation dynamics. In *Metapopulation Biology: Ecology, Genetics and Evolution*, eds. I.A. Hanski and M.E. Gilpin, pp. 27–42. San Diego: Academic Press.
- Henle, K., P. Poschlod, C. Margules, and J. Settele. 1996. Species survival in relation to habitat quality, size and isolation: Summary conclusions and future directions. In *Species Survival in Fragmented Landscapes*, edited by J. Settele, C. Margules, and P. Poschlod, pp. 373–381. Dordrecht: Kluwer Academic Publishers.
- Hobbs, R.J. 1991. Disturbance a precursor to weed invasion in native vegetation. *Plant Protection Quarterly* 6: 99–104.
- Hobbs, R.J. 1993. Effects of landscape fragmentation on ecosystem processes in the western Australian wheatbelt. *Biological Conservation* 64: 193–201.
- Hobbs, R. 1998. Impacts of land use on biodiversity in southwestern Australia. In *Landscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems*, eds. P.W. Rundel, G. Montenegro, and F.M. Jaksic, pp. 81–106. Berlin: Springer-Verlag.
- Hobbs, R.J., and L. Atkins. 1988. The effect of disturbance and nutrient addition on native and introduced annuals in the western Australian wheatbelt. *Australian Journal of Ecology* 13: 171–179.
- Holt, R.D. 1992. A neglected facet of island biogeography: The role of internal spatial dynamics in area effects. *Theoretical Population Biology* 41: 354–371.
- Holt, R.D. 1997. From metapopulation dynamics to community structure: Some

- consequences of spatial heterogeneity. In *Metapopulation Biology: Ecology, Genetics and Evolution*, eds. I.A. Hanski and M.E. Gilpin, pp. 149–164. San Diego: Academic Press.
- Holt, R.D., and M.S. Gaines. 1993. The influence of regional processes on local communities: Examples from an experimentally fragmented landscape. In *Patch Dynamics*, eds. S.A. Levin, T.M. Powell, and J.H. Steele, pp. 260–276. New York: Springer-Verlag.
- Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* 5: 173–185.
- Kapos, V., E. Wandelli, J.L. Camargo, and G. Ganade. 1997. Edge-related changes in environment and plant responses due to forest fragmentation in central Amazonia. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, eds. W.F. Laurance and R.O. Bierregaard, pp. 33–44. Chicago: University of Chicago Press.
- Klein, B.C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70: 1715–1725.
- Landsberg, J., J. Morse, and P. Khanna. 1990. Tree dieback and insect dynamics in remnants of native woodlands on farms. *Proceedings of the Ecological Society of Australia* 16: 149–165.
- Laurance, W.F., L.V. Ferreira, J.M. Rankin-de Merona, and S.G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* 79: 2032–2040.
- Laurance, W.F., L.V. Ferreira, J.M. Rankin-de Merona, S.G. Laurance, R. Hutchings, and T. Lovejoy. 1998. Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* 12: 460–464.
- Laurance, W.F., and C. Gascon. 1997. How to creatively fragment a landscape. *Conservation Biology* 11: 577–579.
- Laurance, W.F., C. Gascon, and J.M. Rankin-de Merona. 1999. Predicting the effects of habitat destruction on plant communities: A test of a model using Amazonian trees. *Ecological Applications* 9: 548–554.
- Laurance, W.F., S.G. Laurance, L.V. Ferreira, J.M. Rankindemerona, C. Gascon, and T.E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. *Science* 278: 1117–1118.
- Laurance, W.F., and E. Yensen. 1991. Predicting the impact of edge effects in fragmented habitats. *Biological Conservation* 55: 77–92.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* 15: 237–240.
- Lovejoy, T.E., R.O. Bierregaard, A.B. Rylands, J.R. Malcolm, C.E. Quintela, L.H. Harper, K.S. Brown, A.H. Powell, G.V.N. Powell, H.O.R. Schubart, and M.B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. In *Conservation Biology: The Science of Scarcity and Diversity*, ed. M.E. Soulé, pp. 257–285. Sunderland, Mass.: Sinauer.
- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*, Princeton, N.J.: Princeton University Press.

- Malcolm, J. R. 1991. *The Small Mammals of Amazonian Forest Fragments: Pattern and Process*. Thesis, University of Florida.
- Malcolm, J.R. 1994. Edge effects in central Amazonian forest fragments. *Ecology* 75: 2439.
- Margules, C.R. 1999. Conservation planning at the landscape scale. In *Issues in Landscape Ecology*, eds. J.A. Wiens and M.R. Moss, pp. 83–87. Boulder, Colo.: International Association for Landscape Ecology, Pioneer Press.
- Margules, C.R., G.A. Milkovits, and G.T. Smith. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonium squama* and an amphipod. *Ecology* 75: 2033–2042.
- Margules, C.R., and A.O. Nicholls. 1987. Assessing the conservation value of remnant habitat “islands”: Mallee patches on the western Eyre Peninsula, South Australia. In *Nature Conservation: The Role of Remnants of Native Vegetation*, eds. D.A. Saunders, G.W. Arnold, A.A. Burbidge, and A.J.M. Hopkins, pp. 89–102. Chipping Norton, Sydney, Australia: Surrey Beatty and Sons.
- McIntyre, S., and S. Laval. 1994. Predicting richness of native, rare and exotic plants in response to habitat disturbance variables across a variegated landscape. *Conservation Biology* 8: 521–531.
- Mesquita, R.C.G., P. Delamonica, and W.F. Laurance. 1999. Effect of matrix type on edge-related tree mortality in Amazonian forest fragments. *Biological Conservation* 91: 129–134.
- Murcia, C. 1995. Edge effects in fragmented forests: Implications for conservation. *Trends in Ecology and Evolution* 10: 58–62.
- Myers, N., R. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Keats. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Oostermeijer, J.G.B., A. Berholz, and P. Poschlod. 1996. Genetical aspects of fragmented populations: A review. In *Species Survival in Fragmented Landscapes*, eds. J. Settele, C. Margules, P. Poschlod, and K. Henle, pp. 93–110. Dordrecht: Kluwer Academic Publishers.
- Parsons, J.J. 1972. Spread of African pasture grasses to the American tropics. *Journal of Range Management* 25: 12–24.
- Pearson, S.M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology* 8: 3–18.
- Powell, A.H., and G.V.N. Powell. 1987. Population dynamics of euglossine bees in Amazonian forest fragments. *Biotropica* 19: 176–179.
- Pressey, R.L., C.J. Humphries, C.R. Margules, R.I. Vane-Wright, and P.H. Williams. 1993. Beyond opportunism: Key principles for systematic reserve selection. *Trends in Ecology and Evolution* 8: 124–128.
- Redpath, S.M. 1995. Habitat fragmentation and the individual: Tawny owls, *Strix aluco*, in woodland patches. *Journal of Animal Ecology* 64: 652–661.
- Robinson, S. K., F. R. Thompson, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987–1990.
- Sarre, S. 1995. Mitochondrial DNA variation among populations of *Oedura reticulata* (Reptilia: gekkonidae) in remnant vegetation: Implications for metapopulation structure and population decline. *Molecular Ecology* 4: 395–405.

- Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5: 18–32.
- Saurez, A.V., D.T. Bolger, and T.J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal Southern California. *Ecology* 79: 2041–2056.
- Scougall, S.A., J.D. Majer, and R.J. Hobbs. 1993. Edge effects in grazed and ungrazed western Australian wheatbelt remnants in relation to ecosystem reconstruction. In *Nature Conservation 3: Reconstruction of Fragmented Ecosystems, Global and Regional Perspectives*, eds. D.A. Saunders, R.J. Hobbs, and P.R. Ehrlich, pp. 163–178. Sydney, Australia: Surrey Beatty and Sons.
- Soulé, M.E., D.T. Bolger, A.C. Alberts, R.S. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology* 2: 75–92.
- Steinberg, E. K., and P. Kareiva. 1997. Challenges and opportunities for empirical evaluation of “spatial theory.” In *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*, eds. D. Tilman and P. Kareiva, pp. 318–332. Princeton, N.J.: Princeton University Press.
- Stouffer, P.C., and R.O. Bierregaard. 1995. Use of Amazonian forest fragments by understory insectivorous birds. *Ecology* 76: 2429–2445.
- Tewksbury, J.J., S.J. Heil, and T.E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79: 2890–2903.
- Viana, V., A.A.J. Tabanez, and J.L.F. Batista. 1997. Dynamics and restoration of forest remnants in the Brazilian Atlantic moist forest. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, eds. W.F. Laurance and R.O. Bierregaard, pp. 351–365. Chicago: University of Chicago Press.
- Whitmore, T.C. 1997. Tropical forest disturbance, disappearance, and species loss. In *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, eds. W.F. Laurance and R.O. Bierregaard, pp. 3–12. Chicago: University of Chicago Press.
- Yates, C.J., and R.J. Hobbs. 1997. Temperate eucalypt woodlands: A review of their status, processes threatening their persistence and techniques for restoration. *Australian Journal of Botany* 45: 949–973.
- Yates, C.J., R.J. Hobbs, and L. Atkins. 2000. Establishment of perennial shrub and tree species in degraded *Eucalyptus salmonophloia* (Salmon gum) remnant woodlands: Effects of restoration treatments. *Restoration Ecology* 8: 135–143.

CONSERVATION PRIORITIES FOR SOIL AND SEDIMENT INVERTEBRATES

Diana H. Wall, Paul V. R. Snelgrove, and Alan P. Covich

Recent syntheses compare the soil and sediment domains of terrestrial, freshwater, and marine ecosystems in terms of biodiversity and their role in ecosystem functioning (Brussaard et al. 1997; Palmer et al. 1997; Snelgrove et al. 1997; Wall Freckman et al. 1997; Covich et al. 1999; Groffman and Bohlen 1999; Snelgrove 1999; Wall and Moore 1999). These reviews suggest that much of the biodiversity in soils and sediments is yet to be described. Although soils and sediments are critical components of almost every habitat on Earth, and numerous species contribute to many ecosystem processes (e.g., nutrient cycling, carbon storage, etc.), little is known of the role that biodiversity plays in ecosystem processes. We first provide a brief description of soils and sediments, the associated biodiversity, and what is known about the relationships of biodiversity to ecosystem processes. This description summarizes evidence of the important role that soil and sediment biota play in sustaining ecosystem processes and, hence, human welfare. The remainder of the chapter discusses how these biota are affected by global change (human activities and accelerating rates of disturbances). We then provide our views on the priorities for conservation and protection of the organisms found in Earth's least explored ecosystems, its soils and sediments.

The Domains

Soils and sediments are finite resources. Hundreds of years may be required to form a centimeter of soil or sediment. Through geologic time, climate, parent material, topography, and biota have contributed to the physical and chemical characteristics that are the key elements of soil and sediment habitats (Anderson 1975; Swift et al. 1979; Wall Freckman et al. 1997; Clark et al. 1999; Kump et al. 2000). In freshwater and marine environments, the direction, magnitude, and variability of water flow, which are influenced by topography and climate, are also important regulators of smaller-scale patterns in sedimentary habitats. The same variables that act over geologic time to develop soils and sediments also act locally on very short time scales. For example, these living organisms have an immediate impact on the characteristics of the soil and sediment in which they reside, through bioturbation, repackaging sediment and soil particles as fecal pellets, and, in death, by contributing organic matter to the ecosystem (Levinton 1995).

The habitats of soils and sediments are amazingly diverse at small and large spatial scales. A few cubic millimeters can contain hundreds of species of microscopic organisms (bacteria, fungi, protozoa, rotifers, tardigrades, nematodes, mites, and many other small invertebrates). At scales of meters and kilometers, larger invertebrates and vertebrates add to the species richness of these habitats. Similarly, the quality and quantity of organic matter, sediment/soil composition and geochemistry, rate of disturbance, climate, and geological history are all factors that contribute to local- and regional-scale patterns of species diversity and abundance among soil and benthic (aquatic, bottom-living) organisms (Snelgrove and Butman 1994; Brussaard et al. 1997; Covich et al. 1999; Wall and Virginia 2000). On a global scale, variability in geologic parent materials and climates has created highly productive soils that are used intensively for agriculture (1.44 billion hectares of a total 13.02 billion hectares) (WRI 1994).

The remaining soils, some 89 percent of terrestrial land, are either not productive due to high salinity, permafrost, or other conditions, or are marginal land that is being modified for short-term use in agriculture. Moreover, approximately 65 percent of the earth's surface is covered in sediments at ocean depths at which no photosynthetic production occurs (Snelgrove 1999).

These soils and sediments cover most of the earth's surface and support a tremendous diversity of species that are a source of ecosystem services needed to maintain life on Earth (Wardle 1995; Brussaard et al. 1997; Costanza et al. 1997; Daily et al. 1997; Palmer et al. 1997; Snelgrove et al. 1997; Wall Freckman et al. 1997; Edinger et al. 1998). In addition to providing a diversity of habitats for below-surface organisms, soils and sediments support food chains that ultimately yield the food (fisheries, crops), fuel, and fiber upon

which civilization depends. The biota of soil and sedimentary environments helps maintain processes in above-ground habitats that have high recreational and aesthetic value, such as forests, deserts, wetlands, rivers, and coastal waterways. Protection and restoration of these subsurface communities are essential if ecosystems are to continue to function and provide ecosystem services.

Unfortunately, many human activities are rapidly accelerating the degradation of soils, sediments, and their biota. Globally, the disruption of soils (e.g., through agricultural practices and construction) has rapidly increased erosion and transport of particles into the atmosphere, rivers, and coastal marine ecosystems, with adverse effects on biota and ecosystem functioning. Coral reefs and their accompanying biota are being rapidly destroyed by increased nutrients from terrestrial ecosystems (Edinger et al. 1998; Naylor et al. 1998; Wagener et al. 1998; Harvell et al. 1999; Hixon et al. 2001; Ewel et al. in press). As productive soils become nutrient depleted or lost through erosion, other natural ecosystems (e.g., forests and wetlands) are claimed for agriculture.

The high demand for coastline property, for development of housing, industry, and aquaculture, has accelerated the loss of coastal wetlands as natural habitats (Levin et al. in press; Ewel et al. in press). Fishing trawls and dredges sweep across the ocean floor creating swaths of highly disturbed bottom habitat (Dayton et al. 1995; Watling and Norse 1998), and dredging of coastal waterways to maintain harbors degrades benthic communities. Some sedimentary taxa are more resilient to disturbance than others (e.g., Prena et al. 1999). For example, organisms in dynamic sandy bottoms frequently moved around by currents may be less vulnerable than species living where physical disturbance is rare (e.g., Watling and Norse 1998). Deep-sea sedimentary communities are more vulnerable to fishing impact than their shallow-water counterparts because deep-sea sedimentary species typically produce few offspring, attain reproductive maturity at a relatively late age, and grow relatively slowly (Merrett and Haedrich 1997). These short-term actions of disturbance have long-term effects on soil and sediment biodiversity and ecosystem processes that affect ecosystem services at local and global scales.

Ecosystem Functioning and Services

Soil and sediment biota contribute many services that are beneficial to humans beyond the value of food production (tables 6.1–6.4; Costanza et al. 1997; Daily et al. 1997; Wall and Virginia 2000). Organisms directly and indirectly drive processes such as nutrient mineralization, nitrogen fixation, hydrologic processes, oxygenation, soil and sediment structure and

stabilization, remediation, burial and/or remobilization of pollutants, and redistribution and decomposition of organic matter (Wall Freckman et al. 1997; Bardgett and Chan 1999; Snelgrove et al. 2000).

Soils and sediments (including deep marine sediments) are the world's largest reservoir of carbon. Therefore, decomposition of organic matter into inorganic forms is a major ecosystem process involving a diversity and succession of organisms (Anderson 1975; Schlesinger 1997). In terrestrial ecosystems, with the exception of grazed, agricultural, and logged lands, most net primary production is returned to soil in the form of organic matter (roots and plant litter). In deep freshwater and marine ecosystems, much of the primary production is provided by phytoplankton that eventually reaches the bottom. In many shallow freshwater ecosystems and nearshore marine areas, macrophytes within the ecosystems, and detrital plant material transported in from adjacent domains, are primary sources of organic matter for detritivores and decomposers.

In all of these subsurface ecosystems, groups such as nematodes and protozoans influence bacterial production and affect rates of decomposition and mineralization (Anderson et al. 1981; Denton et al. 1999). Many groups of invertebrates, such as earthworms, millipedes, isopods, nematodes, and Collembola in soils; polychaetes, molluscs, and crustaceans in marine sediments; and insects, crustaceans, oligochaetes and nematodes in freshwater sediments, move organic matter and microbes through the soil and sediments. These bioturbators that move materials and fluids also provide pathways for diffusion of gases and oxygenate the soils and sediments, contributing to the microbial degradation process through favoring the more efficient aerobic over anaerobic decomposition (e.g., Aller 1983; Kristensen et al. 1992; Coleman and Crossley 1996; Gilbert et al. 1998). Thus, microbial productivity is enhanced by the feeding activity of organisms that obtain their nutrition by ingesting sediments and attached microbes, a phenomenon called microbial gardening (Hilleberg 1975; Grossman and Reichardt 1991).

Biodiversity

The majority (potentially 95 percent) of the species in soil and sediment domains are thought to be undescribed, particularly in marine ecosystems (Wall Freckman et al. 1997). Invertebrates are the major component of known soil and sediment species richness, with larger macroinvertebrates (e.g., arthropods, annelids) contributing the largest numbers of described species. However, it is the smallest organisms (e.g., fungi, bacteria, protozoa, nematodes, mites) with the least numbers of described species that are estimated to have the greatest species diversity, based on recent analyses in habitats using both molecular and morphological techniques (Behan-Pelletier and Newton 1999; Wall and Virginia 2000).

TABLE 6.1. Terrestrial Soil Habitats, Services, and Vulnerability

Habitat	Diversity ^a	Ecosystem Services	Key Taxa	Threats	Global Area	Habitat Degradation
Deserts	Very low to low	Decay, water filtering, stabilizing	Algae, termites ants, bacteria	Exotics, salinization, erosion	Large	Medium
Tropical forests	Medium to very high	Soil fertility, decay, water filtering, soil structure, stabilization	Mycorrhizae, termites, ants earthworms, mites, fungi	Agriculture, cutting, exotics	Large	High
Temperate forests	Low	Decay, water filtering, soil structure, stabilization, sediment trapping	Earthworms, mites, fungi, ants	Acidification, agriculture, cutting, erosion, exotics	Medium	High
Grasslands	High	Herbivory, soil fertility, water filtering, carbon storage, pest control	Earthworms enchytraeids, termites, nematodes, bacteria	Agriculture, overgrazing, urbanization, desertification	Medium	Low
Agriculture	Low	Soil quality	Mycorrhizae, plant pathogens	Reforestation	Low	High

^aKnown diversity. Diversity comparisons are within rather than across domains.

TABLE 6.2. Marine Sedimentary Habitats, Services, and Vulnerability

Habitat	Diversity ^a	Ecosystem Services	Key Taxa	Threats	Global Area	Habitat Degradation
Estuaries	Low	Nutrient cycling, production, bioremediation, water filtering	Bacteria, fish, macroinverts	Pollution, exotics, fisheries	Low	High
Mangels	Low	Nutrient cycling, production, shore stability, sediment trapping, water filtering	Bacteria, plants, fish, macroinverts	Habitat loss, pollution, exotics	Low	Very high
Salt Marshes	Low	Nutrient cycling, production, shore stability, bioremediation, sediment trapping, water filtering	Bacteria, plants, fish, macroinverts	Habitat loss, exotics, pollution,	Low	Very high
Shelf	Low-high	Nutrient cycling, production,	Bacteria, fish, macroinverts	Fishing, habitat loss	Large	Medium
Deep Sea	Very high	Nutrient cycling	Bacteria, macroinverts	—	Very large	Low

^aKnown diversity. Diversity comparisons are within rather than across domains.

TABLE 6.3. Freshwater Sedimentary Habitats, Services, and Vulnerability

Habitat	Diversity ^a	Ecosystem Services	Key Taxa	Threats	Global Area	Habitat Degradation
Deep lakes	High	Production, sediment storage	Fish, amphipods, gastropods	Pollution, overfishing, exotics,	Low	Low
Shallow lakes	Medium	Production, nutrient cycling, sediment trapping	Fish, microbes, macrophytes	Acidification, overfishing, exotics	High	Medium
Rivers	High	Production, flood control, nutrient cycling, sediment transport	Fish, mussels, microbes	Dams, levees, exotics, pollution	Low	High
Reservoirs	Medium	Production, flood control, nutrient cycling, sediment transport	Fish, mussels, microbes, decapods	Diversion, pollution, exotics, overfishing	Medium	Low-high
Springs	High	Water supply	Microbes, macrofauna	Pollution, diversion	High	Low-high
Ponds and wetlands	Low	Nutrient cycling, flood control	Macrophytes, invertebrates	Land use, exotics	Medium	Medium-high
Groundwater	High	Water supply	Microbes, invertebrates	Diversion	High	Low

^aKnown diversity. Diversity comparisons are within rather than across domains.

TABLE 6.4. Ecosystem Services Provided by Soil and Sediment Biota

Regulation of major biogeochemical cycles
Retention and delivery of nutrients to plants and algae
Generation and renewal of soil and sediment structure and soil fertility
Bioremediation of wastes and pollutants
Provision of clean drinking water
Modification of the hydrological cycle, including mitigation of floods and droughts, and erosion control
Translocation of nutrients, particles, and gases
Regulation of atmospheric trace gases (e.g., CO ₂ , NO _x) (production and consumption)
Modification of anthropogenically driven global change (e.g., carbon sequestration, modifiers of plant and algae responses)
Regulation of animal and plant (including algae, macrophyte) populations
Control of potential agricultural pests and vertebrate pathogens
Contribution to plant production for food, fuel, and fiber and to fisheries for food
Contribution to landscape heterogeneity
Vital component of habitats important for recreation and natural history

Source: Modified from G. C. Daily, P. A. Matson, P. M. Vitousek. "Ecosystem Services Supplied by Soil," in *Nature's Services: Societal Dependence on Natural Ecosystems*, G. C. Daily, ed., pp. 113–132 (Washington, D.C.: Island Press, 1997); D. H. Wall, G. Adams, and A. N. Parsons, "Soil Biodiversity under Global Change Scenarios," in *Scenarios of Future Biodiversity*, O. Sala, F. S. Chapin III, and E. Huber-Sannwald, eds. (New York: Springer-Verlag, in press); D. H. Wall and R. A. Virginia, "The World Beneath Our Feet: Soil Biodiversity and Ecosystem Functioning," in *Nature and Human Society: The Quest for a Sustainable World*, P. R. Raven and T. Williams, eds., pp. 225–241 (Washington, D.C.: National Academy of Sciences and National Research Council, 2000).

There are large differences among soils, freshwater sediments, and marine sediments in terms of numbers of species within the different phyla (figure 6.1). Species richness is extremely high in all three domains, and diversity patterns are determined by several factors (Bardgett et al. in press). Most major groups of freshwater species are much less diverse than their marine counterparts. This difference is illustrated in the subphylum Crustacea (phylum Arthropoda): most of the 780 species of mysids are marine; worldwide, only 25 species occur in freshwater, and 18 additional species live in freshwater caves. Generally, only about 10 percent of the nearly 40,000 extant crustacean species occur in the inland pools, lakes, and streams of the world (Thorp and Covich 1991). Some groups such as gastropods, bivalves, and amphipods are exceptionally diverse in inland waters, especially in deep, ancient lakes, caves, and rivers (Allan and Flecker 1993; Martens 1997; Ricciardi and Rasmussen 1999; Culver et al. 2000; Master et al. 2000).

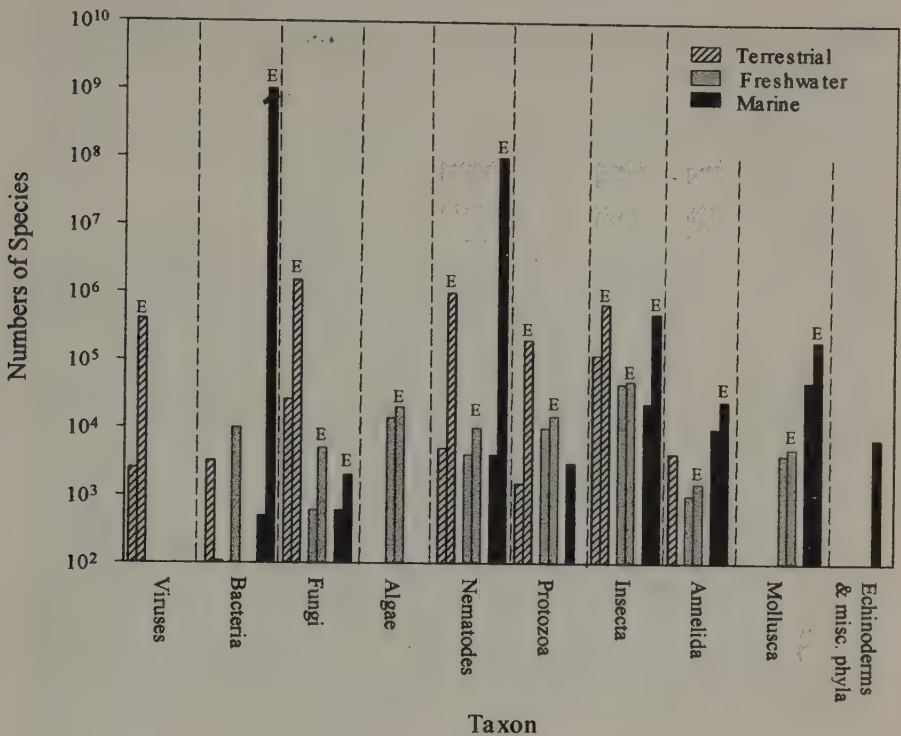


FIGURE 6.1. Estimated numbers of different taxa from terrestrial, freshwater, and marine soils and sediments. Bars denote global estimates of numbers of species already described; those with "E" above them denote extrapolated numbers. Sources for data are Brussaard et al. 1997; Palmer et al. 1997; Snelgrove et al. 1997; and Wall and Virginia 2000.

How does above-surface diversity influence soil and sediment biodiversity? There is insufficient evidence at present to answer this question fully. It appears, however, that (1) above-surface disturbances generally reduce local soil and sediment biodiversity (Freckman and Ettema 1993; Wardle 1995; Covich et al. 1996; Ettema et al. 1999; Wall Freckman et al. 1997); (2) soil and freshwater sediment biodiversity generally is not correlated with latitudinal gradients of plant diversity (Hooper et al. 2000); and (3) marine sediment diversity shows a latitudinal gradient (Rex et al. 1993; Roy et al. 1998). The mechanistic linkages are just being explored for the above- and below-ground (air-soil, water-sediment) components of ecosystems (Hooper et al. 2000; Palmer et al. 2000; Snelgrove et al. 2000). Communities in soils resemble above-surface diversity in that a few species are common and the majority of species are rare (Denton et al. 1999; Wall and Virginia 2000); however, rare

species appear to be more characteristic of marine sediments than of the water column above them (McGowan and Walker 1985; Carney 1997).

Global Change Threats to Ecosystem Functioning and Ecosystem Services

Overview on Species Loss

Here we examine the evidence for the effect of some drivers of global change (invasive species, pollution, habitat destruction, and elevated CO₂) on soil and sediment species and ecosystem functioning. Although little knowledge exists about the functional attributes of the majority of individual species in soil and sediment communities or how their loss affects soil and sediment processes (Schimel 1995; Brussaard et al. 1997; Covich et al. 1999; Bardgett et al. in press), there is information on the effects of larger species on soils and sediments. Macrofaunal species have significant consequences on physical structure and hydrology of soils and sediments over larger spatial (e.g., forest floor, lake, coastal harbor) or temporal scales. Examples of well-documented recent extinctions and endangerment of species in soil or sediment ecosystems are rare, although disappearances of individual species from parts of their pre-human ranges are known, especially for endemic species with limited geographical ranges such as freshwater bivalves (Master et al. 2000).

Invasive Species

Some of the best examples of the potential impacts of shifts in biodiversity on ecosystem functioning are from research on invasive species. In these studies, the focus has often been on the impact of a single species rather than effects of changes in biodiversity per se (Trudgill et al. 1994; Boag et al. 1998; Boag et al. 1999). The global movement of goods over greater distances and at faster speeds than ever before has greatly increased the number of species invasions into soils and sediments, with resulting impacts on biodiversity and ecosystem functioning, and on economics and ecosystem services (Vitousek, Mooney, et al. 1997; Strayer et al. 1999; McMahon 2000).

Although marine environments would appear at first glance to have few barriers to prevent the transport and natural spreading of species, the open ocean is a major barrier to the dispersal of many coastal species. Coastal waters, which have the most numerous and well studied exotic species, are the major focus of most research on introduced species in marine ecosystems (Nichols et al. 1986; Hixon et al. 2001). The predominant mechanism of colonization of coastal benthic species is through transport in the ballast water of ships (Carlton 1985, 2000). Vessels take on ballast water in one port, along with the repro-

ductive propagules, juveniles, and even adults of coastal sedimentary species, and dump it when they arrive in another port. This mechanism has been a major means of inadvertent introductions of exotic species in the Great Lakes and marine coastal waters (Mills et al. 1993; Mackie 2000). As with terrestrial species, physical and chemical barriers as well as biological barriers (such as the presence of predators or strong competitors) limit range expansions of species into inland waters. Species with diapausing stages can be dispersed passively by wildlife and people, as microscopic larvae are transported in bait buckets by fishermen and releases occur from the aquarium trade.

There are numerous examples of accidental or deliberate species introductions that have changed some aspect of the below-surface ecosystem (e.g., biogeochemistry, species diversity, soil or sediment structure), and these disruptions are magnified throughout the whole ecosystem. In most cases, deliberate introductions have been ecologically catastrophic; they have rarely been beneficial.

A number of freshwater and marine species have deliberately been introduced into developing countries for aquaculture, and, although these species often have increased protein availability and economic markets, they are causing environmental degradation (Naylor et al. 1998; Naylor et al. 2000). Significant impacts on the sedimentary fauna of these and neighboring ecosystems occur as a result of the activities of the industries themselves and through biological interactions between native and non-native species. Unfortunately, little research effort is being directed toward this question, which affects many developing countries, even as the scale of aquaculture increases.

Introductions of animals and plants have impacts on the physical and chemical properties of soil and sediment habitats, and indirectly on other soil and sediment biota. For example, an introduced earthworm species in New York forests changed organic matter composition, water infiltration patterns, and soil chemistry (Burtelow et al. 1998). Even the introduction of two exotic plant species, *Berberis thunbergii* and *Microstegium vimineum*, into North American forests has affected soil pH and organic matter and increased earthworm population densities and, subsequently, soil porosity (Kourtev et al. 1998). The periwinkle *Littorina littorea*, introduced from Europe in the early 1800s (Carlton 1982) has displaced the mudsnail *Ilyanassa obsoleta* from New England salt marshes and seagrass beds. Mudsnails are now confined to sand and mudflats that periwinkles cannot utilize, with potential impacts on other species (Brenchley and Carlton 1983). In the soils of the United Kingdom and northern Europe, the invasion of the Australasian planarian flatworm *Artioposthia triangulata*, a predator of earthworms, is causing great

concern (Boag et al. 1998). The flatworm has no known beneficial impact on soils, while earthworms are a source of food for birds and other animals, as well as maintaining soil structure and improving water infiltration. In North America, all soil flatworms are introduced (Ogren and Kawakatsu 1998). Amazonian forest converted to pasture resulted in a 68 percent decrease in the original soil macrofaunal community and a 90 percent dominance in biomass of the colonizing earthworm, *Pontoscolex corethrurus*. This species has an identifiable type of burrowing and casting, which explained the reduction in soil macroporosity from 3 to 1.5 cm³/100g soil and increased bare ground in pasture areas (Chauvel et al. 1999).

Invasive species in freshwater ecosystems represent some of the clearest examples of how dramatically ecosystem functioning can be altered by accidental introduction of a single non-native species. One of the best-known examples is that of the zebra mussel, *Dreissina polymorpha*, a suspension-feeding bivalve native to the Caspian Sea that was inadvertently introduced into the Great Lakes sometime around 1988. Within the Great Lakes it has attained densities that greatly exceed those achieved by native bivalves in rivers and lakes, and it has altered entire aquatic ecosystems as it spreads through watersheds in the United States (Strayer et al. 1999; McMahon 2000). Because zebra mussels attain extraordinarily high densities and filter feed very efficiently, they can effectively strip rivers and lakes of phytoplankton, with significant impacts on food webs, frequency and composition of phytoplankton blooms, nutrient cycling, and water flow (Strayer et al. 1999).

The best-studied examples of inadvertent marine introductions are in San Francisco Bay, where hundreds of non-native species now flourish (Carlton 2000), compressing the habitat of native species and substantially changing the biology of the bay. The explosion of the filter-feeding Asian clam *Potamocorbula amurensis* has greatly increased the capacity of ocean organisms to remove suspended particles, including phytoplankton that is the base of much of the food chain. As a result, the seasonal phytoplankton blooms that characterized the bay have been heavily dampened (Alpine and Cloern 1992), along with other impacts on the pelagic biota (Kimmerer et al. 1994).

Pollution

Pollution affects soil and sediment biodiversity, as well as soil chemical and physical properties, and can have long-term effects on the functioning of ecosystems. As human populations increase, levels of many pollutants have continued to rise (Vitousek, Aber, et al. 1997; Downing et al. 1999). Increased awareness has reduced the rate of input of many compounds, such as pesticides and heavy metals, but persistence of compounds in soils and sediments continues to create problems locally and globally. Agricultural fertilizers

entering surface and ground waters result in the decline of many soil and benthic species. Estuaries are affected by coastal pollution and eutrophication (inputs of phosphorous and nitrogen) because human populations along coasts are rapidly increasing (Ewel et al. in press).

Nutrient enrichment via sewage discharge, storm drainage, and over-application of fertilizers on land and subsequent runoff into freshwater and coastal areas is a major problem. Increased nutrients in aquatic ecosystems favor algal blooms that sink to the bottom, where their decomposition renders the water anoxic. These events are increasingly occurring across domains from midwestern farm soils to the Mississippi drainage and Gulf of Mexico (Turner and Rabalais 1994; Justiz et al. 1997; Malakoff 1998; Downing et al. 1999).

Land-Use Change, Habitat Destruction, and Harvesting

Anything (e.g., tillage, erosion, plant removal) that changes the soil structure, microclimate, physical and chemical properties, and carbon/nitrogen food base of soil food webs (e.g., plant chemical composition, quality and quantity of detritus, oil spills, manure) can have a direct impact on soil diversity and food web structure. Land-use change, the conversion of natural systems to managed systems (as in agriculture, forestry, grazing, urbanization, industrialization), has the greatest effect on soil biota, because it generally decreases the diversity of all soil taxa and dramatically changes the primary determinants of soil biodiversity, e.g., soil structure, vegetation, and microclimate (Wall et al. in press). For example, Lawton et al. (1998) found that species richness of nematodes and termites, as well as six other above-ground animal groups, declined with increasing disturbance in a Cameroon forest. The species decline was most obvious in active slash-and-burn areas and cleared tropical forest.

Intensive tillage can result in decoupling of nutrient release from plant uptake and a need for greater amounts of fertilizer. Efforts to conserve soils by methods such as reduced tillage and no tillage have beneficial effects of increasing soil carbon storage, improving soil moisture, and decreasing disruptions of soil food webs. However, reduced tillage methods may require increased inputs of herbicides and result in increased densities of soil pathogens (bacteria, fungi, nematodes, some insects). The banning of many nematicides and fungicides, such as methyl bromide and DBCP, due to their adverse environmental effects, has reduced the arsenal of pesticides used to manage soil pathogens for the past fifty years (Duncan and Noling 1998). The demand for new control measures for soil pathogens that allow maintenance of plant productivity under reduced tillage systems presents a new research and management challenge.

The wetlands of the world, both freshwater and marine, have suffered major destruction in the last few centuries. In marine ecosystems, the greatest habitat loss is occurring in coastal environments, particularly transition zones, or regions where soil and freshwater domains meet marine habitats. Transition zones are critical habitats for many species, and the sedimentary organisms that reside within them provide an important food resource. Destruction of mangrove habitats for shrimp farming and other forms of coastal development result in the loss of habitat and food for many species (Beveridge et al. 1994; Naylor et al. 2000; Ewel et al. in press).

Climate and Elevated CO₂

Increased frequency of extreme climatic events predicted as a result of global change can have varying effects on soil and sediment biota (Boag et al. 1991; Covich et al. 1997; Schindler 1997; Hogg et al. 1998; Sala et al. 2000; Smith et al. in press; Wall et al. in press; Wolters et al. in press). Climate change, increasing elevated atmospheric CO₂, and the resulting changes in rainfall patterns, soil temperatures, and plant performance are predicted to alter the geographical distribution of soil species indirectly through changes in vegetation distribution (Groffman and Bohlen 1999; Wall et al. in press; Wolters et al. in press). Frequency and amount of rainfall can increase populations of soil pathogenic fungi by reducing soil aeration, resulting in shifts in species composition and richness.

Ecosystem-level effects of climate change on soil biodiversity are just beginning to be analyzed through manipulative experiments that increase elevated CO₂ and vary rainfall and temperature. Direct effects of elevated CO₂ on soil organisms are considered to be less important than indirect effects, because most soils naturally have higher than ambient CO₂ concentrations due to root respiration. Indirect effects on soil biota have occurred through changes in plant metabolism, resulting in reallocation of carbon and nitrogen. Increased below-ground plant resources affect both decomposition and herbivory (Zak et al. 1996).

There are many projections of the indirect effect of global-change drivers on freshwater ecosystems (Covich 1993; Kolar and Lodge 2000). For example, in increasingly arid regions increasing human demands will result in construction of more dams and irrigation canals. These structures will increase habitat fragmentation and alter disturbance regimes, refugia, and microhabitats of freshwater species. Alteration of rates and direction of water flow for irrigation has a major impact on terrestrial, freshwater, and coastal marine ecosystems; hydrological changes impact soil and sediment composition, pH of water and soils, and salinity, among other variables (Strange et al. 1999). Dam construction in the southeastern United States constitutes one of the largest threats to persistence of freshwater species, especially bivalves

(Bogan 1993; Master et al., 2000). There are about 334 species of freshwater bivalves in North America. The recent loss of many of these bivalve species and the invasion of inland waters by non-native bivalves represent major challenges for ecosystem management.

Little direct evidence suggests that biodiversity changes among marine sedimentary organisms are attributed to global climate change, but studies of pelagic and intertidal communities (Southward et al. 1995) and seagrass communities (Marba and Duarte 1997) suggest that effects may be expected. One of the most serious projections in some global-warming scenarios for marine sedimentary fauna is the possible shifting of ocean currents (Manabe et al. 1994), which influence food supply and transport of reproductive propagules from bottom-dwelling species.

Conservation Research Priorities

Policy makers, the public, and national and international trade and economic organizations have yet to realize that soil and sediment biota are interlinked with the above surface we see, or to realize that the biodiversity in soils and sediments contributes to ecosystem services and goods that help drive economics and benefit humanity. Much of this wealth is as yet undescribed, mapped, or recognized as a new world for exploration. Yet evidence suggests that the destruction of soil and sediment habitats changes biodiversity with cascading effects on ecosystem processes and endangers the ability of the biota to maintain goods and services. These habitats and their biodiversity cannot be easily restored.

Protection and conservation of soil and sediment biodiversity are dependent on an increase in education, research, and publicity to address the gaps in the scientific knowledge of species distributions, impacts of global-change drivers, and consequences for goods and services. Education at all levels must incorporate more opportunities for learning about the role of biodiversity in soils and sediments and how these subsurface habitats are linked to each other and to above-ground habitats. Soils, sediments, and invertebrate biodiversity, particularly biodiversity at the microscopic level, can become more relevant to students if the traditionally taught biology curriculum in elementary schools, high schools, and colleges is changed to include more comprehensive approaches to understanding how ecosystems function and the importance of nutrient cycling, decomposition, and the complex physical and chemical environment. Such an approach would increase understanding of our dependence on multiple species in soil and sediments. This would incorporate new technologies and a sense of discovery into classrooms and field trips. The separation of chemistry and biology as different subjects and the isolation of related topics on atmospheric and earth sciences prevents most students from a comprehensive understanding of the important roles that

many different microbial and macroscopic species have in regulating rates of ecosystem processes.

Most people of any age recognize their “own” ecosystem (backyard, garden, soil, city, stream, park, field), but, in many classrooms, the local environment and its interactions, functions, and linkages to regional or global ecosystems are given limited time. Nor is there discussion of how individuals or human activities contribute to the conservation, sustainable management, and restoration of an essential natural resource: soils, including freshwater and marine sediments. Most high school and college curricula in biology today are focused on premedical perspectives, and that important information dominates discussion of the overall relationships of emerging diseases and sustainable food production and availability of clean waters.

New technologies (e.g., GIS, molecular analysis) are rapidly advancing the study of biodiversity in soils and sediments when, unfortunately, the number of systematists globally has declined. It is now possible to geo-reference soils with global positioning systems as they are sampled; extract different invertebrate groups; then rapidly sort the numerous individuals from many families using microscopes with enhanced computer image analysis; and integrate the data with other related GIS data on soil physical and chemical characteristics, vegetation, and disturbance factors (Oliver et al. 2000). The study of species in soils and sediments is further advanced with the use of molecular tools, which contribute to both taxonomic and ecological research such as faster assessments of geographic distribution patterns, phylogenetic relationships, and consequences of disturbance (e.g., effect of climate change on below-surface organisms and ecosystem processes). Incorporating these new techniques for estimating soil and sediment biodiversity into existing research efforts at aquatic and terrestrial sites will enhance and broaden the quantitative information on ecosystem functioning and lead to better recommendations for conservation, restoration, and sustainability.

We offer the following statements as a basis for the research priorities summarized in box 6.1:

- Although we know very little about the diversity and composition of most soil and sediment communities, we do have detailed studies of some species.
- We do know that soil and sediment communities perform functions that are critical for the functioning of the ecosystem as a whole, although the role of biodiversity in those processes is poorly understood.
- The number of taxonomists specializing in below-surface species has declined when our abilities to learn about these species have increased with new technologies.

- Soils and sediments are being altered by acceleration of rates of inputs of nutrients and organic matter and by physical disruption or destruction of habitats.
- The public is generally unaware of the essential ecosystem services provided by subsurface organisms.

BOX 6.1. Summary of Research Priorities for Soil and Sediment Ecosystems

1. Develop a strategy to increase the numbers of systematists working with below-surface invertebrates, as there are presently very few of these specialists globally.
2. Develop a strategic approach to better represent and understand the functions of poorly sampled taxa (e.g., bacteria, protozoa, fungi, nematodes) and geographic areas (e.g., tropical soils, tropical shallow- and deep-sea sediments) to generate species estimates for these habitats with a greater degree of certainty.
3. Identify which taxa and habitats are most vulnerable to biodiversity loss, including those areas that represent hot spots of biodiversity and ecosystem services within soils and sediments.
4. Determine which soil and sediment habitats are most amenable to restoration once degraded, and the mechanisms and time scales by which they may be most effectively restored.
5. Document linkages between different soil and sediment domains, between communities above and below the soil/sediment-water interface, and between natural versus human-dominated systems, and how changes in one system may influence another.
6. Identify aspects of the natural history of key taxa as they compare to other species that may fill similar ecological niches, with the goal of evaluating whether functional redundancy actually exists within different soil and sediment ecosystems and whether species loss will have significant functional consequences to the ecosystem.
7. Using natural history information, predict which species are likely to be invasive, thus offering potential strategies to reduce their spread and evaluate which species and services may be most at risk to invasive species.
8. Improved budgets for global processes, such as carbon and nitrogen cycling, where the traditional approach of treating species as black boxes is replaced with an effort to determine the role played by individual species in these key processes.

Linking Conservation and Research Priorities

Many soil and sedimentary ecosystems have been degraded by human activities, both in terms of the biodiversity within these systems and the ecosystem services that they provide. As scientists, we are just beginning to communicate to the general public and policy makers regarding the potential gravity of these threats to global sustainability. Experiments are needed to provide essential data as to the degree of linkages and dependency of ecosystem processes on soil and sediment species under current environmental conditions, and the role biological diversity plays in ensuring continued ecosystem functioning under scenarios of global change. New research can provide a detailed analysis of soil and sedimentary organisms, their value, and their contribution to ecosystem services.

We do know that there are certain processes in which a diversity of soil and sedimentary organisms are integral players, and we know in some instances that certain species are critical to those processes. However, our level of scientific knowledge on soil and sediment organisms is insufficient. The majority of data on linkages between soil and sediment species is for a single species and a single effect, and there are few data on multiple species across diverse taxonomic groups within a community, their interactions and effects on ecosystem processes. Although biodiversity is very likely being lost, we, at present, cannot predict where and when the loss will have minor or catastrophic consequences. In some instances, scientists may expect that policy implementation will follow a precautionary principle, but in the majority of instances, it will be necessary to provide irrefutable data to demonstrate that as human activities affect soil and sedimentary systems at an accelerating rate, conservation principles are in the best interests of individuals, communities, and nations.

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LITERATURE CITED

- Allan, J. D., and A. S. Flecker. 1993. Biodiversity conservation in running waters: Identifying the major factors that threaten destruction of riverine species and ecosystems. *BioScience* 43:32–43.

- Aller, R. C. 1983. The importance of the diffusive permeability of animal burrow linings in determining marine sediment chemistry. *Journal of Marine Research* 41:299–322.
- Alpine, A. E., and J. E. Cloern. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37:946–955.
- Anderson, J. M. 1975. Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. *Journal of Animal Ecology* 44:475–494.
- Anderson, R. V., D. C. Coleman, C. V. Cole, and E. T. Elliott. 1981. Effect of the nematodes *Acrobeloides* sp. and *Mesodiplogaster iheritierii* on substrate utilization and nitrogen and phosphorus mineralization in soil. *Ecology* 62:549–555.
- Bardgett, R. D., J. M. Anderson, V. Behan-Pelletier, L. Brussaard, D. C. Coleman, C. Ettema, A. Moldenke, J. P. Schimel, and D. H. Wall. In press. The influence of soil biodiversity on hydrologic pathways and the transfer of materials between terrestrial and aquatic ecosystems. *Ecosystems*.
- Bardgett, R. D., and K. F. Chan. 1999. Experimental evidence that soil fauna enhance nutrient mineralization and plant nutrient uptake in montane grassland ecosystems. *Soil Biology & Biochemistry* 31:1007–1014.
- Behan-Pelletier, V., and G. Newton. 1999. Linking soil biodiversity and ecosystem function: The taxonomic dilemma. *Bioscience* 49:149–152.
- Beveridge, M. C. M., L. G. Ross, and L. A. Kelly. 1994. Aquaculture and biodiversity. *Ambio* 23:497–502.
- Boag, B., J. W. Crawford, and R. Neilson. 1991. The effect of potential climatic changes on the geographical distribution of the plant-parasitic nematode *Xiphinema* and *Longidorus* in Europe. *Nematologica* 37:312–323.
- Boag, B., H. D. Jones, R. Neilson, and G. Santoro. 1999. Spatial distribution and relationship between the New Zealand flatworm *Arthurdendyus triangulata* and earthworms in a grass field in Scotland. *Pedobiologia* 43:340–344.
- Boag, B., G. W. Yeates, and P. M. Johns. 1998. Limitations to the distribution and spread of terrestrial flatworms with special reference to the New Zealand flatworm (*Artioposthia triangulata*). *Pedobiologia* 42:495–503.
- Bogan, A. E. 1993. Freshwater bivalve extinctions (Mollusca, Unionoida)—A search for causes. *American Zoologist* 33:599–609.
- Brenchley, G. A., and J. T. Carlton. 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. *Biological Bulletin* 165:543–558.
- Brussaard, L., V. M. Behan-Pelletier, D. E. Bignell, V. K. Brown, W. Didden, P. Folgarait, C. Fragoso, D. W. Freckman, V. Gupta, T. Hattori, D. L. Hawksworth, C. Klopatek, P. Lavelle, D. W. Malloch, J. Rusek, B. Soderstrom, J. M. Tiedje, and R. A. Virginia. 1997. Biodiversity and ecosystem functioning in soil. *Ambio* 26:563–570.
- Burtelow, A., P. J. Bohlen, and P. M. Groffman. 1998. Influence of exotic earthworm invasion on soil organic matter, microbial biomass and denitrification potential in forest soils of the northeastern U.S. *Applied Soil Ecology* 9:197–202.

- Carlton, J. T. 1982. The historical biogeography of *Littornia littorea* on the Atlantic coast of North America, and implications for the interpretation of the structure of New England intertidal communities. *Malacological Review* 15:146.
- Carlton, J. T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. *Oceanography and Marine Biology: An Annual Review* 23:313–371.
- Carlton, J. T. 2000. Global change and biological invasions. In *Invasive Species in a Changing World*, eds. H. A. Mooney and R. J. Hobbs, pp. 31–53. Washington, D.C.: Island Press.
- Carney, R. S. 1997. Basing conservation policies for the deep-sea floor on current-diversity concepts: A consideration of rarity. *Biodiversity and Conservation* 6:1463–1485.
- Chauvel, A., M. Grimaldi, E. Barros, E. Blanchart, T. Desjardins, M. Sarrazin, and P. Lavelle. 1999. Pasture damage by an Amazonian earthworm. *Nature* 398:32–33.
- Clark, P. U., R. B. Alley, and D. Pollard. 1999. Climatology—Northern hemisphere ice-sheet influences on global climate change. *Science* 286:1104–1111.
- Coleman, D. C., and D. A. Crossley. 1996. *Fundamentals of Soil Ecology*. San Diego: Academic Press.
- Costanza, R., R. d'Arge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. Oneill, J. Paruelo, R. G. Raskin, P. Sutton, and M. vandenBelt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–260.
- Covich, A. P. 1993. Water and ecosystems. In *Water in Crisis: A Guide to the World's Fresh Water Resources*, ed. P. H. Gleick, pp. 40–55. Oxford: Oxford University Press.
- Covich, A. P., T. A. Crowl, S. J. Johnson, and M. Pyron. 1996. Distribution and abundance of tropical freshwater shrimp along a stream corridor: Response to disturbance. *Biotropica* 28:484–492.
- Covich, A. P., S. C. Fritz, P. J. Lamb, R. D. Marzolf, W. J. Matthews, K. A. Poiani, E. E. Prepas, M. B. Richman, and T. C. Winter. 1997. Potential effects of climate change on aquatic ecosystems of the Great Plains of North America. *Hydrological Processes* 11:993–1021.
- Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. The role of benthic invertebrate species in freshwater ecosystems: Zoobenthic species influence energy flows and nutrient cycling. *Bioscience* 49:119–127.
- Culver, D. C., L. L. Master, M. C. Christman, and H. H. Hobbs, III. 2000. Obligate cave fauna of the 49 contiguous United States. *Conservation Biology* 14:386–397.
- Daily, G. C., P. A. Matson, and P. M. Vitousek. 1997. Ecosystem services supplied by soil. In *Nature's Services: Societal Dependence on Natural Ecosystems*, ed. G. C. Daily, pp. 113–132. Washington, D.C.: Island Press.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5:205–232.

- Denton, C. S., R. D. Bardgett, R. Cook, and P. J. Hobbs. 1999. Low amounts of root herbivory positively influence the rhizosphere microbial community in a temperate grassland soil. *Soil Biology & Biochemistry* 31:155–165.
- Downing, J. A., M. McClain, R. Twilley, J. M. Melack, J. Elser, N. N. Rabalais, W. M. Lewis, R. E. Turner, J. Corredor, D. Soto, A. Yanez-Arancibia, J. A. Kopaska, and R. W. Howarth. 1999. The impact of accelerating land-use change on the N-Cycle of tropical aquatic ecosystems: Current conditions and projected changes. *Biogeochemistry* (Dordrecht) 46:109–148.
- Duncan, L. W., and J. W. Noling. 1998. Agricultural sustainability and nematode integrated pest management. In *Agronomy Monograph 36*, eds. K. R. Barker, G. A. Pederson, and G. L. Windham, pp. 251–287. Madison, WI: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America.
- Edinger, E. N., J. Jompa, G. V. Limmon, W. Widjatmoko, and M. J. Risk. 1998. Reef degradation and coral biodiversity in Indonesia: Effects of land-based pollution, destructive fishing practices and changes over time. *Marine Pollution Bulletin* 36:617–630.
- Ettema, C. H., R. Lowrance, and D. C. Coleman. 1999. Riparian soil response to surface nitrogen input: Temporal changes in denitrification, labile and microbial C and N pools, and bacterial and fungal respiration. *Soil Biology & Biochemistry* 31:1609–1624.
- Ewel, K. C., C. Cressa, R. T. Kneib, P. S. Lake, L. A. Levin, M. Palmer, P. Snelgrove, and D. H. Wall. In press. Managing critical transition zones. *Ecosystems*.
- Freckman, D. W., and C. E. Ettema. 1993. Assessing nematode communities in agroecosystems of varying human intervention. *Agriculture, Ecosystems and Environment* 45:239–261.
- Gilbert, F., G. Stora, and P. Bonin. 1998. Influence of bioturbation on denitrification activity in Mediterranean coastal sediments: An in situ experimental approach. *Marine Ecology Progress Series* 163:99–107.
- Groffman, P. M., and P. J. Bohlen. 1999. Soil and sediment biodiversity: Cross-system comparisons and large-scale effects. *Bioscience* 49:139–148.
- Grossman, S., and W. Reichardt. 1991. Impact of *Arenicola marina* on bacteria in intertidal sediments. *Marine Ecology Progress Series* 77:85–93.
- Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofman, E. K. Lipp, A. D. M. E. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith, and G. R. Vasta. 1999. Emerging marine diseases—Climate and anthropogenic factors. *Science* 285:1505–1510.
- Hixon, M. A., E. A. Norse, M. L. Hunter Jr., P. D. Boersma, F. Micheli, H. P. Possingham, and P. V. R. Snelgrove. 2001. Oceans at risk: Research priorities in marine conservation biology. In *Conservation Biology: Research Priorities for the Next Decade*, eds. M. E. Soulé and G. H. Orians, pp. 125–154.
- Hogg, I. D., J. M. Eadie, and Y. de Lafontaine. 1998. Atmospheric change and the diversity of aquatic invertebrates: Are we missing the boat? *Environmental Monitoring and Assessment* 49:291–301.

- Hooper, D. U., D. E. Bignell, V. K. Brown, L. Brussaard, J. M. Dangerfield, D. H. Wall, D. A. Wardle, D. C. Coleman, K. E. Giller, P. Lavelle, W. H. van der Putten, P. C. de Ruiter, J. Rusek, W. Silver, J. Tiedje, V. Wolters. 2000. Interactions between above and belowground biodiversity in terrestrial ecosystems: Patterns, mechanisms, and feedbacks. *Bioscience* 50:1049–1061.
- Hylleberg, J. 1975. Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. *Ophelia* 14:113–137.
- Justiz, D., N. N. Rabalais, and R. E. Turner. 1997. Impact of climate change on net productivity of coastal waters: Implications for carbon budgets and hypoxia. *Climate Change* 8:225–237.
- Kimmerer, W. J., E. Gartside, and J. J. Orsi. 1994. Predation by an introduced clam as the likely cause of substantial declines in zooplankton of San Francisco Bay. *Marine Ecology Progress Series* 113:81–93.
- Kolar, C., and D. M. Lodge. 2000. Freshwater nonindigenous species: Interactions with other global changes. In *Invasive Species in a Changing World*, eds. H. Mooney and R. Hobbs, pp. 3–30. Washington, D.C.: Island Press.
- Kourtev, P. S., J. G. Ehrenfeld, and W. Z. Huang. 1998. Effects of exotic plant species on soil properties in hardwood forests of New Jersey. *Water Air and Soil Pollution* 105:493–501.
- Kristensen, E., F. O. Andersen, and T. H. Blackburn. 1992. The effects of benthic macrofauna and temperature on degradation of macroalgal detritus: The fate of organic carbon. *Limnology and Oceanography* 37:1404–1419.
- Kump, L. R., S. L. Brantley, and M. A. Arthur. 2000. Chemical weathering, atmospheric CO₂, and climate. *Annual Review of Earth and Planetary Sciences* 28:611–667.
- Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* (London) 391:72–76.
- Levin, L. A., D. F. Boesch, A. P. Covich, C. Dahm, C. Erséus, K. C. Ewel, R. T. Kneib, M. Moldenke, M. A. Palmer, P. Snelgrove, D. Strayer, and J. M. Weslawski. In press. The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems*.
- Levinton, J. 1995. Bioturbators as ecosystem engineers: Control of the sediment fabric, inter-individual interactions, and material fluxes. In *Linking Species and Ecosystems*, eds. C. G. Jones and J. H. Lawton, pp. 29–36. London: Chapman and Hall.
- Mackie, G. L. 2000. Ballast water introductions of Mollusca. In *Nonindigenous Freshwater Organisms*, eds. R. Claudi and J. H. Leach, pp. 219–254. Boca Raton, Fla.: Lewis Publishers.
- Malakoff, D. 1998. Death by suffocation in the Gulf of Mexico. *Science* 281:190–192.
- Manabe, S., R. J. Stouffer, and M. J. Spelman. 1994. Response of a coupled ocean-atmosphere model to increasing atmospheric carbon dioxide. *Ambio* 23:44–49.
- Marba, N., and C. M. Duarte. 1997. Interannual changes in seagrass (*Posidonia oceanica*) growth and environmental change in the Spanish Mediterranean littoral zone. *Limnology and Oceanography* 42:800–810.

- Martens, K. 1997. Speciation in ancient lakes. *Trends in Ecology and Evolution* 12:177–182.
- Master, L. L., B. A. Stein, L. S. Kutner, and G. A. Hammerson. 2000. Vanishing assets: The conservation status of U.S. species. In *Precious Heritage: The Status of Biodiversity in the United States*, eds. B. A. Stein, L. S. Kutner, and J. S. Adams, pp. 93–118. New York: Oxford University Press.
- McGowan, J. A., and P. W. Walker. 1985. Dominance and diversity maintenance in an oceanic ecosystem. *Ecological Monographs* 55:105–118.
- McMahon, R. F. 2000. Invasive characteristics of the freshwater bivalve *Corbicula fluminea*. In *Nonindigenous Freshwater Organisms*, eds. R. Claudi and J. H. Leach, pp. 315–343. Boca Raton, Fla.: Lewis Publishers.
- Merrett, N. R., and R. L. Haedrich. 1997. *Deep-Sea Demersal Fish and Fisheries*. London: Chapman and Hall.
- Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19:1–54.
- Naylor, R. L., R. J. Goldberg, H. Mooney, M. Beveridge, J. Clay, C. Folke, N. Kautsky, J. Lubchenco, J. Primavera, and M. Williams. 1998. Nature's subsidies to shrimp and salmon farming. *Science* 282:883–884.
- Naylor, R. L., R. J. Goldberg, J. H. Primavera, N. Kautsky, M. C. M. Beveridge, J. Clay, C. Folke, J. Lubchenco, H. Mooney, and M. Troell. 2000. Effect of aquaculture on world fish supplies. *Nature* 405:1017–1024.
- Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. *Science* 231:567–573.
- Ogren, R. E., and M. Kawakatsu. 1998. American nearctic and neotropical land planarians (Tricladida: Terricola) faunas. *Pedobiologia* 42:441–451.
- Oliver, I., S. Pik, D. Britton, J. M. Dangerfield, R. K. Colwell, and A. J. Beattie. 2000. Virtual biodiversity assessment systems. *BioScience* 50:441–450.
- Palmer, M. A., A. P. Covich, B. J. Finlay, J. Gibert, K. D. Hyde, R. K. Johnson, T. Kairesalo, P. S. Lake, C. R. Lovell, R. J. Naiman, C. Ricci, F. F. Sabater, and D. L. Strayer. 1997. Biodiversity and ecosystem processes in freshwater sediments. *Ambio* 26:571–577.
- Palmer, M. A., A. P. Covich, S. Lake, P. Biro, J. J. Brooks, J. Cole, C. Dahm, J. Gibert, W. Goedkoop, K. Martens, J. Verhoeven, and W. J. van de Bund. 2000. Linkages between aquatic sediment biota and life above sediments as potential drivers of biodiversity and ecological processes? *Bioscience* 50:1062–1075.
- Prena, J., P. Schwinghamer, T. W. Rowell, D. C. Gordon, K. D. Gilkinson, W. P. Vass, and D. L. McKeown. 1999. Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: Analysis of trawl bycatch and effects on epifauna. *Marine Ecology—Progress Series* 181:107–124.
- Rex, M. A., C. T. Stuart, R. R. Hessler, J. A. Allen, H. L. Sanders, and G. D. F. Wilson. 1993. Global-scale latitudinal patterns of species diversity in the deep-sea benthos. *Nature* (London) 365:636–639.
- Ricciardi, A., and J. B. Rasmussen. 1999. Extinction rates of North American freshwater faunas. *Conservation Biology* 13:1220–1222.

- Roy, K., D. Jablonski, J. W. Valentine, and G. Rosenberg. 1998. Marine latitudinal diversity gradients: Tests of causal hypotheses. *Proceedings of the National Academy of Sciences of the United States of America* 95:3699–3702.
- Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. Jackson, A. Kinzig, R. Leemans, D. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walkder, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Schimel, J. 1995. Ecosystem consequences of microbial diversity and community structure. *Ecological Studies* 113:239–254.
- Schindler, D. W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. *Hydrological Processes* 11:1043–1067.
- Schlesinger, W. H. 1997. *Biogeochemistry: An Analysis of Global Change*. San Diego: Academic Press.
- Smith, C. R., M. C. Austen, G. Boucher, C. Heip, P. A. Hutchings, G. M. King, I. Koike, P. J. D. Lamshead, and P. Snelgrove. 2000. Global change and biodiversity linkages across the sediment-water interface. *Bioscience* 50:1108–1120.
- Snelgrove, P. V. R. 1999. Getting to the bottom of marine biodiversity: Sedimentary habitats: Ocean bottoms are the most widespread habitat on earth and support high biodiversity and key ecosystem services. *Bioscience* 49:129–138.
- Snelgrove, P. V. R., M. C. Austen, G. Boucher, C. Heip, P. A. Hutchings, G. M. King, I. Koike, P. J. D. Lamshead, and C. R. Smith. 2000. Linking biodiversity above and below the marine sediment-water interface. *Bioscience* 50:1076–1088.
- Snelgrove, P. V. R., T. H. Blackburn, P. A. Hutchings, D. M. Alongi, J. F. Grassle, H. Hummel, G. King, I. Koike, P. J. D. Lamshead, N. B. Ramsing, and V. Solis-Weiss. 1997. The importance of marine sediment biodiversity in ecosystem processes. *Ambio* 26:578–583.
- Snelgrove, P. V. R., and C. A. Butman. 1994. Animal-sediment relationships revisited: Causes versus effect. *Oceanography and Marine Biology: An Annual Review* 32:111–177.
- Southward, A. J., S. J. Hawkins, and M. T. Burrows. 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* 20:127–155.
- Strange, E. M., K. D. Fausch, and A. P. Covich. 1999. Sustaining ecosystem services in human-dominated watersheds: Biohydrology and ecosystem processes in the South Platte River basin. *Environmental Management* 24:39–54.
- Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves: A case study of zebra mussels in the Hudson River. *Bioscience* 49:19–27.
- Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. *Decomposition in Terrestrial Ecosystems*. Oxford: Blackwell.
- Thorp, J. H., and A. P. Covich. 1991. *Ecology and Classification of North American Freshwater Invertebrates*. San Diego: Academic Press.

- Trudgill, D., V. Blok, M. Phillips, S. Gowen, and M. Hahn. 1994. The importance of understanding the centres of origins of nematode pests. *Aspects of Applied Biology* 39:133–138.
- Turner, R. E., and N. N. Rabalais. 1994. Coastal eutrophication near the Mississippi River delta. *Nature* 368:619–621.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7:737–750.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277:494–499.
- Wagener, S. M., M. W. Oswood, and J. P. Schimel. 1998. Rivers and soils: Parallels in carbon and nutrient processing. *BioScience* 48:104–108.
- Wall, D. H., G. Adams, and A. N. Parsons. In press. Soil biodiversity. In *Future Scenarios of Global Biodiversity*, eds. F. S. Chapin III, O. E. Sala, and E. Huber-Sannwald. New York: Springer-Verlag.
- Wall, D. H., and J. C. Moore. 1999. Interactions underground: Soil biodiversity, mutualism, and ecosystem processes. *BioScience* 49:109–117.
- Wall, D. H., and R. A. Virginia. 2000. The world beneath our feet: Soil biodiversity and ecosystem functioning. In *Nature and Human Society: The Quest for a Sustainable World*, eds. P. R. Raven and T. Williams, pp. 225–241. Washington, D.C.: National Academy of Sciences and National Research Council.
- Wall Freckman, D., T. H. Blackburn, L. Brussaard, P. Hutchings, M. A. Palmer, and P. V. R. Snelgrove. 1997. Linking biodiversity and ecosystem functioning of soils and sediments. *Ambio* 26:556–562.
- Wardle, D. A. 1995. Impacts of disturbance on detritus food webs in agro-ecosystems of contrasting tillage and weed management practices. *Advances in Ecological Research* 26:105–183.
- Watling, L., and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conservation Biology* 12:1180–1197.
- Wolters, V., W. L. Silver, D. E. Bignell, D. C. Coleman, P. Lavelle, W. van der Putten, P. de Ruiter, J. Rusek, D. H. Wall, D. A. Wardle, L. Brussaard, J. M. Dangerfield, V. K. Brown, K. E. Giller, D. U. Hooper, O. Sala, J. Tiedje, and J. A. van Veen. 2000. Global change effects on above- and belowground biodiversity in terrestrial ecosystems: Interactions and implications for ecosystem functioning. *BioScience* 50:1089–1098.
- WRI (World Resources Institute). 1994. *World Resources 1994–1995*. New York: Oxford University Press.
- Zak, D. R., D. B. Ringelberg, K. S. Pregitzer, D. L. Randlett, D. C. White, and P. S. Curtis. 1996. Soil microbial communities beneath *Populus grandidentata* grown under elevated atmospheric CO₂. *Ecological Applications* 6:257–262.

OCEANS AT RISK

Research Priorities in Marine Conservation Biology

Mark A. Hixon, P. Dee Boersma,
Malcolm L. Hunter Jr., Fiorenza Micheli, Elliott A. Norse,
Hugh P. Possingham, and Paul V. R. Snelgrove

*In the end, we will conserve only what we love.
We will love only what we understand.*

—Baba Dioum, Senegalese naturalist and poet

The marine environment encompasses a broad array of ecosystems, ranging from spectacular coral reefs and kelp forests to coastal mangroves, seagrass beds, and salt marshes; to expansive deep-sea plains interspersed with trenches, seamounts, ridges, and hydrothermal vents; to the vast open water column up to thousands of meters deep. Although the oceans cover 70.8 percent of the earth's surface, we know little about the three levels of biodiversity in the sea: genetic, species, and ecosystem (Norse 1993; NRC 1995; McAllister 1996; Ormond et al. 1997). However, we do know that marine biodiversity is extremely valuable to humankind, accounting for over 60 percent of the economic value of the biosphere (Costanza et al. 1997). Sea life provides five basic services to humans (Norse 1993; Daily 1997; Costanza 1999; Moberg and Folke 1999):

- *Ecosystem services.* Examples range from the global "biological pump" that sequesters atmospheric carbon dioxide and transports carbon to the deep sea, to the regional role of coral reefs and salt marshes in moderating coastal erosion.
- *Food.* About 20 percent of the animal protein consumed by humans comes from marine fisheries.
- *Medicines.* Marine organisms are increasingly found to contain biomedically active compounds, including antitumor agents.
- *Minerals and chemicals.* Examples include abiotic resources (fossil fuels, manganese, table salt, etc.), as well as chemicals derived from organisms (such as alginate from seaweeds and chitin from crustaceans, both used in a broad variety of food, medical, and technological applications).
- *Recreation and ecotourism.* Marine life, especially the charismatic megafauna of the seas (marine mammals, etc.), has inspired humankind since time immemorial. Recreational use of coral reefs supports many regional economies.

Despite their immense value, marine ecosystems are deteriorating rapidly due to human activities, especially physical alteration of habitat, overexploitation, species introductions, global climate change, and marine pollution (reviews by GESAMP 1990; Norse 1993; NRC 1995; Peterson and Estes 2000; Steneck and Carlton 2000). The most threatened systems are coastal, especially wetlands (including estuaries, salt marshes, and mangroves), coral reefs, and communities associated with the seafloor of the continental shelves.

Unfortunately, because detailed exploration of the oceans is a recent endeavor, we have little knowledge of what species are being lost (Irish and Norse 1996). It is nonetheless becoming increasingly clear that human-induced extinction in the sea is a sad and threatening reality (Carlton et al. 1991; Carlton 1993; Norse 1993; Vermeij 1993; Culotta 1994; Vincent and Hall 1996; Malakoff 1997; Casey and Myers 1998; Carlton et al. 1999; Roberts and Hawkins 1999). To date, it has been documented that only four marine snails, five seabirds, and three marine mammals have gone extinct in recent history due to human activities, but these cases are undoubtedly the mere tip of the iceberg of ongoing marine extinctions. Conservative estimates suggest that over 50,000 species of coral-reef organisms have already been lost (Carlton et al. 1999).

The goals of this chapter are twofold. First, we provide a brief review of the major differences between marine and terrestrial systems relevant to conservation biology, emphasizing the present limits of our knowledge. Second,

we propose nine broad scientific research priorities in marine conservation biology, emphasizing six of these as particularly urgent. These priorities were derived from the literature, from canvassing experts (the thirty-five respondents listed in the acknowledgments), and from the workshop participants. Our list extends related research priorities previously proposed by Grassle et al. (1991) (table 7.1) and by the NRC (1995) (table 7.2), as well as the general research thrust described in the Sustainable Biosphere Initiative (Lubchenco et al. 1991). The focus is on natural science rather than socioeconomic issues, although the latter are also crucially important (e.g., Myers and Kent 1998; Costanza et al. 1999; chapter 10). Additionally, we focus more on urgent empirical priorities than on theoretical research questions, even though theory clearly has a role in all conservation efforts.

Addressing research priorities in marine conservation biology will require a broadly based interdisciplinary approach, including oceanography, toxicology, physiology, genetics, paleontology, taxonomy, systematics, and ecology.

TABLE 7.1. Research Questions Regarding Marine Biodiversity Previously Reported by Grassle et al. (1991).

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1. Is the spectrum of environmental variation in marine and terrestrial ecosystems fundamentally different?
 2. Are biogeographic patterns of biodiversity and ecosystem function determined by a combination of environmental patterns (i.e., are single-factor theories not viable)?
 3. Are offshore primary production and nutrient cycling dominated by pelagic processes that determine biogeographic differences in biodiversity?
 4. Do increases in environmental heterogeneity in space and time, including disturbance, increase biodiversity, especially in the coastal zones?
 5. Do keystone species play a more important role in marine than in terrestrial ecosystems, and is that role more important in the lower latitudes?
 6. Do species introductions have major consequences for marine ecosystem function?
 7. Are extinctions less likely to occur in marine than in terrestrial systems?
 8. Are increases in airborne and waterborne pollutants (including terrestrially derived disease species) and/or overfishing currently resulting in widespread changes in marine systems?
 9. Have marine ecosystems and organisms developed less robust internal processes to respond to the low-magnitude short-term variations, and would this result in a reduced ability to respond to large-scale environmental changes?
 10. Is redundancy of genes and species necessary for the long-term survival of marine ecosystems?
 11. Is there greater genetic variation at the molecular level within species in marine environments than in terrestrial ones?
-

Source: F. Grassle, P. Lasserre, A. D. McIntyre, and G. C. Ray, "Marine Biodiversity and Ecosystem Function: A Proposal for an International Programme of Research." *Biology International* 23 (Special Issue, 1991): 1-19.

TABLE 7.2. Research Questions Regarding Marine Conservation Biology Previously Reported by the National Research Council (1995).

Natural Variation in Biodiversity Pattern and Why Biodiversity Matters

1. How do genetic, species, and ecosystem diversity vary in space and time at different regional scales and within habitats within those regions? Examples of specific research questions are:
 - To what extent does the maintenance of local biodiversity (genetic or species) depend on linkages between distant populations, the dispersal between them, and the availability of suitable habitat?
 - How does genetic diversity within a species influence reproduction and population growth or susceptibility to epidemic disease?
 - To what extent do changes in biodiversity at one site within a region—or between regions—affect the biodiversity at another site or in another region?
 - What specific characteristics of a habitat directly or indirectly influence genetic and species diversity? For example, are there parallels in the origin and maintenance of coral reef and deep-sea biodiversity?
2. What is the functional significance of biodiversity at the genetic, species, and ecosystem levels? Are species within a functional group interchangeable? What might be learned from comparing and contrasting systems in terms of the functional significance of biodiversity? (For example, are there parallels between the ecological significance of microbial diversity as coral reef symbionts [zooxanthellae] and as open-ocean primary producers [picoplankton]?)
3. To what extent does the diversity of a community determine (a) “stability,” (b) productivity, (c) resistance to invasion or disease, and (d) ability to recover from natural and human impacts? Equally important, how do these factors interact? Do high-diversity systems have higher or lower production than systems whose diversity has been impaired? What is the role of biological invasions in altering system production or energy flow?
4. How good are the estimates of genetic, species, and ecosystem biodiversity, and how do the limitations (i.e., understanding of the scale of error) influence an understanding of biodiversity patterns and of ecosystem structure and function?

Given the scope of challenges in conserving sea life, we cite key publications to facilitate entry into the marine biodiversity and conservation literature. For recent accounts in the popular press regarding the plight of the seas, we suggest Marx (1999), Thorne-Miller (1999), and Woodard (2000).

Differences between Marine and Terrestrial Conservation Biology

There are substantial ecological differences between the sea and the land (reviews by Steele 1974, 1985; Norse 1993; Cohen 1994; May 1994; NRC 1995; Field et al. 1998), several of which pose contrasts regarding challenges in conservation research:

Human Impact on Processes Responsible for Biodiversity Change

1. What are the direct impacts on biodiversity of human-altered systems? That is, what is the variation in biodiversity over spatial and temporal scales relevant to the critical environmental issues? Examples of specific research questions are:
 - How do human influences on biodiversity differ from those caused by natural processes?
 - To what extent do human effects alter the probability of ecosystem collapse in different systems?
 - To what extent are particular changes in biodiversity due to human activities reversible?
 - Given the often direct impacts on certain target species within a region, are species within functional groups interchangeable within a system?
 - How does the addition or loss of species due to human activities affect community structure and resilience?
2. What are the indirect impacts on biodiversity of human-altered systems? Examples of specific research questions are:
 - What characteristics of species enhance susceptibility or provide immunity to precipitous declines?
 - In what types of habitats are alternative ecological communities stable?
 - Are threshold processes involved in precipitous declines (and the persistence of those declines) in biodiversity, and ultimately, in the risk of extinction of individual species?
 - Does genetic or species diversity provide a buffer against irreversible or massive perturbations?
 - What are the long-term effects of species replacements (e.g., exotic species) on ecosystem function?

Source: National Research Council, *Understanding Marine Biodiversity: A Research Agenda for the Nation* (Washington, D.C.: National Academy Press, 1995).

- *Oceans are huge and difficult to study.* Relative to that of air, the high density of seawater provides greater buoyancy and support for organisms, thereby distributing planktonic (drifting) and nektonic (swimming) sea life over a vast three-dimensional environment. Assuming that the terrestrial biosphere effectively averages 50 m thick, Childress (1983) estimates that the oceans constitute approximately 99.5 percent of the volume of the biosphere (21.0 percent less than 1,000 m deep and 78.5 percent greater than 1,000 m deep). Averaging some 4,000 m in depth and very difficult to access by humans, the abyssal plain is the largest continuous environment on the earth, accounting for about 42 percent of the area of the oceans and about 30 percent of the planet.

Marine biodiversity is high but largely unknown. As the probable original source of life on the earth, the sea has a greater diversity of animal phyla (fifteen phyla are solely marine vs. one solely terrestrial) than the land (Norse 1993; NRC 1995). Newly discovered marine ecosystems have revealed a variety of taxa previously unknown to science. For example, over twenty new families, one hundred new genera, and two hundred new species (with high endemism) have been discovered on and near deep-sea hydrothermal vents (Tunnicliffe 1991; Van Dover 2000). Hundreds of newly discovered species of invertebrates and fishes are described annually (WCMC 1992).

The immense volume of the oceans, combined with the small size of most marine plankton, offers particular challenges in documenting and understanding the diversity of tiny marine organisms. Entire species groups, such as the prochlorophyte picoplankton, have been discovered only recently (Chisholm et al. 1988; Olson et al. 1990). Undiscovered marine microorganisms may comprise at least thirty-four phyla and eighty-three classes (Corliss 1994).

As a consequence of the huge size, the variety of life and habitats, and the inaccessibility of the oceans, estimates of species diversity in the sea are very rough (reviews by WCMC 1992; Norse 1993; NRC 1995). Grassle and Maciolek (1992) estimate that ten million macroscopic animal species inhabit the deep sea. Snelgrove et al. (1997) report that there are some one hundred thousand species described from marine sediments in general, and perhaps one hundred million undescribed species. Reaka-Kudla (1997) estimates that up to nine million species, including about 30 percent of marine fish species (Roberts et al. 2000), inhabit coral reefs. Accounting for less than 1 percent of the ocean surface, coral reefs can be considered the tropical rain forests of the seas in terms of both high biodiversity and threatened status, with 50–70 percent of reefs under direct threat from human activities (Wilkinson 1999).

Genetic diversity among and within marine species is also high, including many cryptic and sibling species, but is very poorly understood (Palumbi 1992, 1994; Knowlton 1993; Avise 1998). The genetic diversity of marine viruses is particularly immense, with typically fifteen to forty visibly distinct genome sizes in a given sample of seawater, including high spatial and temporal variation (Fuhrman 1999). Genetic diversity of marine bacteria is also huge (Giovannoni et al. 1990). Given that less than 15 percent of the approximately 1.7–1.8 million described species worldwide are marine (WCMC 1992; May 1994), we are sorely in need of a comprehensive assessment of marine species

richness and biodiversity. However, immediate conservation action to conserve this diversity is needed before we can afford the time for such an assessment.

- *Marine food webs are extremely complex.* The small size of marine phytoplankton strongly influences the structure of oceanic food webs. Most of the primary production in the sea is consumed by herbivores, unlike the situation on land, where most plant material dies and enters the decomposer food web (detritus nonetheless being the major food input to the deep sea). Indeed, the turnover of phytoplankton can be so high that there can be inverted pyramids of biomass, in which the standing crop of herbivorous zooplankton actually exceeds that of the phytoplankton. Thus, "ecological efficiency," the percentage of energy stored in one trophic level (say, plants) that becomes incorporated in the next higher trophic level (say, herbivores), tends to be greater in the sea than on land (about 20 percent vs. about 10 percent). This fact, combined with the virtual absence of size constraints in marine animals due to the support provided by water, results in marine food webs often having more trophic levels than those on land. Moreover, the relative morphological and evolutionary complexity of marine life results in many cases of omnivory (organisms that consume more than one trophic level below them) and mixotrophy (organisms that both photosynthesize and consume other organisms). These phenomena multiply the number of trophic linkages in marine food webs, creating ecologically complex communities. This complexity, including a variety of direct and indirect interactions, offers challenges in understanding, managing, and conserving marine life at the scale of entire ecosystems (see chapter 3).
- *Oceanic currents transport both larvae and pollutants.* The common reproductive mode of multicellular organisms in the sea (with the exception of sharks, marine mammals, and a few other groups) is broadcast spawning of small gametes, with dispersal occurring during a pelagic (open-water) larval stage. Especially in species that are associated with the seafloor as adults (benthos and demersal fishes), this life history pattern may result in local populations that are largely demographically and genetically open, linked by larval dispersal (a population of populations typically called a metapopulation). However, at some larger spatial scale, all marine populations are reproductively closed (Jones et al. 1999; Swearer et al. 1999). Poorly known is the extent of larval retention within local populations as well as the level of connectivity among populations (Cowen et al. 2000), both of which have important ramifications for conservation of marine species. Larval dispersal may in fact

reduce the risk of extinction in some marine organisms. However, this hypothesis has not been adequately tested, and severe declines in populations of large predatory fishes due to overfishing suggest that reliance on this hypothesis is dangerous. In fact, increasing recognition of large numbers of sibling species in the oceans suggests that there may be substantial subdivision of species and populations (Knowlton 1993). Patterns of larval dispersal between spatially isolated local populations may result in genetically identifiable subpopulations or "stocks" delineated by ocean circulation patterns. At the same time, larval transport creates fluid boundaries between oceanic ecosystems and biogeographic regions. Consequently, geographical ranges of species tend to be larger in the sea than on land (reviews by Norse 1993; NRC 1995; Ormond et al. 1997). The spatial scales of resulting "large marine ecosystems" (Sherman et al. 1990) are typically greater than those of political boundaries, creating management problems for straddling fish stocks and highly migratory fishery species.

Finally, oceanic currents transport chemicals as well as organisms, so that it may be more difficult to contain the spread of both pollutants and exotic species in the sea vs. on land (excluding atmospheric dispersal). The oceans are biogeochemical sinks located downstream from land. Coastal marine ecosystems, particularly near the mouths of major rivers, receive tremendous inputs of terrestrially generated pollutants, especially via agricultural runoff.

Overall, compared to that of its terrestrial counterpart, the science of marine conservation biology is in its infancy for three related reasons: (1) the relative size and inaccessibility of the seas (e.g., SCUBA and research submersibles have been widely used by biologists only since the 1970s); (2) the relatively scant funding of marine conservation (e.g., in FY 1999, the U.S. National Parks Service received US\$1.7 billion in funding, whereas the U.S. National Marine Sanctuary Program received US\$14.3 million); and (3) the relatively sparse literature on this subject (e.g., until recently, terrestrial papers in *Conservation Biology* outnumbered marine papers thirteen to one). Scant funding and sparse literature may be a consequence of the general focus of marine science on issues other than conservation biology. All told, only 0.25 percent of the oceans are afforded some level of conservation protection, compared to over 5 percent of the land (McAllister 1996).

Research Priorities in Marine Conservation Biology

Given our general lack of detailed knowledge relevant to marine conservation biology, research priorities for the next decade (indeed, the next century) include the nature of marine biodiversity, the threats to that biodiversity, and

the tools for conserving life in the sea. Nine research priorities are discussed in sequence below and listed with specific priority actions in box 7.1.

Understanding the Nature of Marine Biodiversity

It is difficult to conserve something that is unknown. The key questions underlying this section are: What are we trying to conserve, and how does it function? As is true on land, substantial efforts at documenting marine biodiversity at the level of ecosystems, species, and genes are important. There is also an urgent need for long-term monitoring of marine ecosystems at multiple spatial scales (e.g., CARICOMP in the Caribbean, Ogden and Gladfelter 1986). (Note, however, that biodiversity assessment and monitoring are not necessarily related, as the latter can focus on only a few indicator species.) Marine taxonomy and systematics must also be revitalized (Winston 1992; Feldmann and Manning 1992; Vecchione and Collette 1996). Less formal but equally important, local cultural knowledge can be a major source of information on marine species and their ecology, as exemplified by Johannes's (1981) studies of Pacific coral reef fishes and fisheries.

However, while immediate estimation of undescribed species richness is an important tool, pursuing long-term monitoring and alpha taxonomy should not delay resolution of urgent conservation issues. Therefore, we advocate a major initiative to organize the spatial and temporal information on marine biodiversity that is already available, constructing databases that will be of immediate use for conservation efforts. Geographic information systems (GIS) mapping patterns of marine habitats and biodiversity will be especially valuable for the establishment of substantial networks of no-take marine reserves. At the same time, we see the importance of intensive ecological studies of several key marine ecosystems. We thus propose three research priorities concerning the nature of marine biodiversity:

- *Map the distribution of and threats to biodiversity (ecosystems, species, genes).* Cataloging the distribution of marine life among ecosystem types is the traditional realm of marine biogeography (Briggs 1974). However, conservation efforts require detailed geographic information systems that overlay different aspects of biodiversity (as well as threats) at nested spatial scales, including species-area relationships (Johnston 1998). This endeavor is the focus of seascape ecology (Bartlett and Carter 1991; Ray 1991; Jones and Andrew 1992). GIS assessments of species richness are already being developed and are proving effective for some taxa, such as coral reef fishes (Roberts et al. 2000). An important issue is whether habitat-generating species (such as corals, large seaweeds) and visually dominant groups (such as fishes, large invertebrates) can provide accurate indices of total diversity

within highly species-rich communities or those that are otherwise difficult to study (Ward et al. 1999).

We emphasize that much of the needed mapping will require not new research but assembly of existing data. Related research is required to determine the most effective ways to map marine habitats and associated biodiversity. Some approaches may be biophysically based, while others may be based on actual species composition at different locations. For select groups of organisms, indirect mapping tools can be ground-truthed by detailed field assessments.

Regarding genetic diversity, marine conservation genetics is in its infancy (Knowlton 1993; Palumbi 1992, 1994; Avise 1998). Expanded use of modern molecular methods will provide insight on population genetics, identify cryptic and sibling species, elucidate levels of endemism, and generate novel measures of genetic biodiversity. Of course, such analyses take time that we can ill afford, so immediate conservation action remains a higher priority than detailed assessments of genetic diversity.

GIS assessments should also incorporate ecosystem diversity, including coastal zones integrated with associated terrestrial systems (Ray and Hayden 1992; Ray 1996). Overall, these tools will identify regions of high species richness and high endemism, spawning and nursery habitats, migration routes, unique or special environments (such as hydrothermal vents), and particularly sensitive ecosystems. Overlying data on the nature, intensity, and urgency of threats to these regions will enable policy makers and managers to choose and rank areas for immediate conservation efforts, as well as identify sites for long-term study and monitoring.

- *Document temporal changes in biodiversity (ecosystems, species) over historical and geological time scales.* Because long-term knowledge of marine communities is lacking for most systems, the status of marine ecosystems and especially our perceptions of their pre-impact baseline conditions are both shifting rapidly (Pauly 1995; Sheppard 1995; Jackson 1997; Dayton et al. 1998; Steneck and Carlton 2000). Increasing evidence suggests that human impacts on marine ecosystems occurred long before the latter half of the twentieth century (reviews by Pauly 1995; Steneck and Carlton 2000). Examples have been documented in Alaska (Simenstad et al. 1978), the Caribbean (Jackson 1997), California (Dayton et al. 1998), the Gulf of Maine (Steneck and Carlton 2000), and elsewhere (Aronson 1990). Continued examination of historical accounts, as well as intensified monitoring, will provide better estimates of recent changes in marine communities and patterns of biodi-

versity. Over longer time scales, the fossil record can provide insight on the relative stability of species assemblages (e.g., Sepkoski 1992; Jackson 1995). Further exploration of existing community-level paleontological data will provide estimates of background rates of extinction in the sea. Such baselines will provide a basis of comparison for modern trends that may help to convince governments of the urgency of marine conservation issues.

- *Explore the ecological mechanisms driving population dynamics, structuring communities, and affecting biodiversity in several key ecosystems.* Despite advances in our knowledge of rocky intertidal communities and other reasonably well-studied systems, we know little of basic population and community ecology as they relate to marine conservation biology. Certainly, such information will come only with time and substantial effort, but this knowledge is crucial for understanding what naturally regulates marine populations and maintains species diversity. We advocate intensive ecological study of several ecologically important and representative systems, including: (1) small open-ocean fishes and krill, which constitute the major trophic links between plankton and high-seas fishery species; (2) coastal bottom-oriented fishes (and the seafloor communities of which they are a part), which are often severely overexploited and their habitats physically altered by trawling (see below); and (3) coral reefs, the most species-rich and among the most threatened of all marine ecosystems (see above).

At the population level, increasing use of genetic methods (Avice 1998), otolith (fish ear-stone) microchemistry (Swearer et al. 1999), larval tagging (Jones et al. 1999), and physical oceanography (Cowen et al. 2000) will answer questions regarding population connectivity, metapopulation structure, and stock boundaries. These issues are particularly important for designing and implementing marine protected areas (see below). The mechanisms driving and regulating population fluctuations in the sea are also largely unknown, although hypotheses abound (Rothschild 1986; Sale 1991; Cushing 1995; Caley et al. 1996). Increasing use of controlled field experiments, especially at larger spatial scales, will be especially informative, but not always possible (Hixon and Webster 2001). Central topics in community ecology relevant to conservation include the roles of habitat complexity, disturbance and succession, webs of direct and indirect interactions, and diversity-stability and diversity-function relationships (conceptual reviews by Huston 1994; Pickett et al. 1998).

Ultimately, such knowledge will allow us to answer crucial questions regarding extinction and conservation in the sea. Is our knowledge of

terrestrial species relevant for conserving marine species (reviews by WCMC 1992; Carlton et al. 1999; Roberts and Hawkins 1999)? Does larval dispersal render marine species less prone to extinction than terrestrial species (Grassle et al. 1991)? What are minimal viable population sizes (review by Soulé 1987)—from both a demographic and a genetic perspective—in marine species with relatively open vs. closed populations? How (if at all) does the Allee effect (a decreasing population growth rate at low population sizes, reviewed by Courchamp et al. 1999) operate in the sea? Are increases in population sizes of protected marine species hastening the decline of other threatened species, such as sea otters contributing to the demise of white abalone in California (Tegner et al. 1996) or orcas causing the decline in sea otters off Alaska (Estes et al. 1998)?

Understanding the Threats to Marine Biodiversity

The ultimate threat to biodiversity in the sea, as on land, is human overpopulation and overconsumption spurred by technological developments, global commerce, ignorance, greed, and inadequate conservation programs. Proximally, there are five major categories of human-induced threats in the oceans (general reviews by GESAMP 1990; Norse 1993; NRC 1995; Botsford et al. 1997; Peterson and Estes 2000; Steneck and Carlton 2000):

- *Physical alteration of habitat.* Marine habitats are physically degraded by (1) coastal development (including mariculture practices that destroy or alter estuaries, salt marshes, and mangroves), dredging, shoreline erosion, and resulting sedimentation; (2) ocean mining and seafloor drilling; and (3) destructive fishing practices, including bottom trawling and dynamite fishing.
- *Overexploitation.* Widespread overfishing of the seas has resulted in stock collapses and alterations of population and community structure.
- *Species introductions.* Transported across the seas attached to ship hulls or contained in ballast water, introduced exotic species have potential competitive, predatory, and biological-disturbance impacts on native species and communities.
- *Marine pollution.* Located downstream from land, the sea carries the burden of human-generated excess nutrients via runoff of sewage and fertilizers (as well as atmospheric deposition of nitrogenous compounds), petroleum spills, halogenated hydrocarbons (pesticides, PCBs, dioxins, etc.), heavy metals, radioactive waste, plastics, etc.
- *Global climate change.* Global warming is altering oceanic currents and patterns of marine productivity, is associated with increasing coral

bleaching, and threatens coastal marine ecosystems via sea level rise, while stratospheric ozone depletion is increasing UV-B penetration in the sea, with documented negative effects on marine organisms.

All these threats are important. We see global climate change as one of the most dangerous threats to marine biodiversity, but due to its universal nature, we defer to the chapter on that topic (chapter 9). Therefore, we advocate focused research priorities within each of the four remaining categories of threats. Despite this separation of impacts into distinct categories, it is important to keep in mind that anthropogenic threats to marine biodiversity are ubiquitous, cumulative, and synergistic, as exemplified by the sorry states of the Baltic Sea (Elmgren 1989), the Black Sea (Zaitsev 1992), and the Caribbean Sea (Hughes 1994). The four remaining categories of threats are as follows:

- *Document how physical alteration and fragmentation of habitats affect seafloor ecosystems.* Seafloor habitats are structured physically by geological and oceanographic processes (resulting in different seafloor types, such as sand vs. rock), and biologically by biogenic habitat builders (species such as mangroves, salt marsh grasses, seagrasses, seaweeds, and corals that create living space for other species), as well as by agents of biological disturbance (such as stingrays digging for buried prey and infaunal clams turning over sediments).

Degradation and outright destruction of the physical structure of habitat is the most direct negative impact of humanity on the seas. Studies to date indicate that nearshore marine populations and communities are negatively affected by human-induced coastal erosion and sedimentation, artificial beach nourishment, and dredging (reviews by Nelson 1993; Maragos et al. 1996; Peterson et al. 2000). About half of all mangroves are already lost, increasingly due to construction of mariculture ponds, mostly for shrimp and prawn production (Fortes 1988; Kaly and Jones 1998). Offshore, where we have fewer data, trawl and dredge fisheries are clearly degrading crucial seafloor environments and communities (reviews by Jones 1992; Dayton et al. 1995; Watling and Norse 1998; Auster and Langton 1999). Between 1976 and 1991, Georges Bank off New England was trawled and dredged an average of 200 to 400 percent of its area annually. In impoverished developing nations, both demand and greed have led to degradation of coral reefs via dynamite, cyanide, and bleach fishing, all devastating forms of Malthusian overfishing (Pauly 1988). This tragedy is exacerbated by a developing "live fish" restaurant and aquarium trade (Johannes and Riepen 1995).

We need more accurate information on the extent of these impacts, the effects they have on biodiversity over different spatial and temporal scales, and how reversible they are. How much more marine habitat—including salt marshes, mangroves, coral reefs, seagrass beds, and kelp forests—can be lost without the substantial loss of associated species? If human impacts are ameliorated, how long will it take these ecosystems to recover (if they ever can)? Regarding habitat fragmentation, we need more information on population dynamics and movements of bottom-living fish and invertebrates among patches of seafloor habitat created by human activities (Butman et al. 1995; Irlandi and Crawford 1997; Micheli and Peterson 1999).

- *Document how overfishing alters marine food webs.* Compared to terrestrial systems, food extracted by humans from the sea comprises wild (rather than domestic) species at high (rather than low) trophic levels (Pauly et al. 1998). There is increasing evidence that the seas are severely overfished (e.g., Dayton et al. 1995; Pauly and Christensen 1995; Safina 1995; Botsford et al. 1997; FAO 1997; Jennings and Kaiser 1998; Pauly et al. 1998; Hall 1999; NRC 1999). The general question is: What are the direct (i.e., demographic and genetic) and indirect (i.e., community and ecosystem) ecological impacts of fishing on marine populations and communities? Direct effects have been the conceptual realm of fishery science, and we have no intention of presumptuously setting research priorities for fisheries management agencies. We are encouraged by ongoing fisheries research designed to predict sustainable levels of exploitation more realistically by increasing the accuracy of stock assessments (NRC 1998). Also encouraging is a trend for fisheries scientists to examine deeper questions regarding the effects of exploitation on both the demography (e.g., Musick, Berkeley, et al. 2000; Musick, Burgess, et al. 2000; Coleman et al. 2000; Parker et al. 2000) and the genetics (e.g., Ryman 1991; Smith et al. 1991) of targeted species.

However, the indirect effects of overfishing on entire marine communities are still seldom addressed due to the historical single-species focus of fishery biology and general lack of funding. Importantly, fished species are parts of larger systems, so altering their abundance often has ramifications for the entire system. Decreases in population sizes of both targeted and bycatch species can result in “biomass dominance shifts,” due to alterations of competitive and predatory interactions (e.g., May et al. 1979; Fogarty and Murawski 1998). In extreme cases, such shifts can lead to systems switching between “alternate stable states” (e.g., Simenstad et al. 1978; Estes et al. 1998). An area of spe-

cial concern is bycatch, which is the capture of nontargeted species by fisheries, and which accounts for about a quarter of the entire marine catch (reviews by Alverson et al. 1994; Hall 1996; Crowder and Murawski 1998). Most bycatch is discarded at sea, which provides a supplemental food source for seabirds, sharks, crabs, and other scavengers, with unknown community-wide consequences. These and other indirect effects of overfishing are examined in detail in chapter 3, but few are well documented and all clearly pose important research priorities.

- *Document how species introductions affect native species and alter community structure.* The largely inadvertent translocation of marine species, both as sessile adults attached to ship hulls and as larvae carried in ballast water, is increasingly well documented, but the ecological impacts of most introduced exotics are poorly known (reviews by Carlton 1985, 1999; Carlton and Geller 1993; Ruiz et al. 1997, 1999). Unfortunately, in many systems we do not always know which species are truly native vs. introduced vs. cryptogenic (of unknown history; Carlton 1996). Indeed, more than one thousand common intertidal and subtidal species may have been introduced by ships worldwide between 1500 and 1800 (Carlton 1999), and an estimated three thousand species are in transit daily in the ballast water of ships (Carlton and Geller 1993). Mariculture programs may introduce not only cultured species, but also their close associates and their diseases (Naylor et al. 2000). The rate at which marine diseases are spread by human activities and especially the consequences (such as the Caribbean-wide pandemic affecting long-spined urchins in the early 1980s; Lessios 1988) are areas of special concern (Harvell et al. 1999).

There is need for the geographic origin of marine species to be elucidated by paleontological data (the recent fossil record; e.g., Pandolfi and Minchin 1995; Pandolfi and Jackson 2001), anthropological information (such as human middens; e.g., Simenstad et al. 1978; Borque 1996), and genetic analyses (Avice 1998). Ultimately, there is need to understand the determinants of whether and how introduced species survive and spread in their new habitats, and whether a successfully invasive introduced species comes to dominate its new habitat via competition, predation, or biological disturbance. Of particular concern are the ecological impacts of genetically modified mariculture species, such as the effects of cultured salmon on wild stocks (Naylor et al. 2000).

- *Document how the increasing scale of human-induced eutrophication alters ecosystems.* Given that the oceans are downstream from land,

there are numerous pollutants in the seas. These include excess nutrients via runoff of sewage and fertilizers (as well as atmospheric deposition of nitrogenous compounds), petroleum spills, halogenated hydrocarbons (pesticides, PCBs, dioxins, etc.), heavy metals, plastics (including abandoned fishing nets), and radioactive waste (GESAMP 1990; Kennish 1998; Sindermann 1996). GESAMP estimates that the sources of marine pollutants are runoff and land-based discharge (44 percent), atmospheric deposition (33 percent), maritime transportation (12 percent), ocean dumping (10 percent), and offshore oil production (1 percent). Most coastal pollutants are deposited directly from the land (runoff), whereas most open-ocean pollutants are deposited from the atmosphere.

While all these pollutants pose substantial threats, we believe that human-induced eutrophication of the seas is the most pressing problem and the highest research priority regarding marine pollution. Human activities now add at least as much fixed nitrogen to terrestrial ecosystems as do all natural sources combined (Schlesinger 1997; Vitousek et al. 1997), and the oceans receive this nitrogenous pollution from both coastal runoff and via atmospheric deposition. The resulting eutrophication induces macroalgal and microbial blooms, some of which are highly toxic (Hallegraeff 1993), produce expanding "dead zones" of decomposing primary producers (Turner and Rabalais 1994), and alter associated marine communities (Diaz and Rosenberg 1995; Burkholder 1998; Micheli 1999). Ample data show how individual sites respond to organic enrichment, but we are less able to predict the consequences of the increasing scale of eutrophication in terms of specific threats to marine species and general effects on ecosystem services.

Taking Action to Conserve Marine Biodiversity

We emphasize that, although we know relatively little about the nature of and threats to marine biodiversity, enough is known to justify immediate conservation action (Ludwig et al. 1993; Costanza et al. 1998). By the time we understand enough about the oceans to implement conservation policies that are strongly empirically based, it may well be too late (see also Johannes 1998). Scientific uncertainty (Ludwig et al. 1993) and the precautionary principle (Earl 1992) dictate that we take substantial conservation action now, preferably in the experimental context of true adaptive management (Walters and Hilborn 1978; Holling 1978). We see the implementation of marine protected areas as the most immediate and effective conservation action, and the development of marine restoration ecology as an important general priority:

- *Implement and evaluate networks of marine protected areas.* Given that less than 0.25 percent of the oceans are now offered some level of protection (McAllister 1996); the immediate implementation of a substantial network of no-take marine reserves is crucial (Murray et al. 1999). Protecting regions of the sea from all direct human impacts prevents physical alteration of habitat, overexploitation, and point-source pollution (but not global climate change or widespread pollution, and perhaps not species introductions). Such ecosystem-based management applies the precautionary principle by conserving entire systems that we do not fully understand (Earl 1992; Ludwig et al. 1993; Griffiths and Kimball 1996; Agardy 1997; Murray et al. 1999; Palumbi 2001).

The first step in implementing reserves is using available data to map regional patterns of habitat and biodiversity, then selecting initial sites for protection (Leslie et al. in press). Identification of both representative and crucial ecosystems for protection (both relatively pristine and degraded) requires detailed GIS assessments (see above). Once provisional networks of no-take marine reserves are in place, we can begin to learn how they function ecologically and, politics permitting, implement adaptive management in terms of evaluating and optimizing the number, size, and spacing of reserves. At present, the rule-of-thumb recommendation is that at least 20 percent of the oceans be protected such that all ecosystems are represented proportionally within no-take reserves (Murray et al. 1999). Currently, the only scientific basis for this percentage is that fishery biologists believe that at least 20 percent of a spawning stock must be conserved to ensure population viability (Bohnsack et al. manuscript). Of course, the siting of reserves is also crucial. For example, conservation of Pacific salmon and other species that migrate between fresh and saltwater will require integrated land-and-sea reserves (see Lichatowich et al. 2000).

Evaluating and optimizing the effectiveness of existing marine reserve networks will require substantial research in several areas *after* reserves are already implemented in an experimental framework. First, knowledge of the level of connectivity of open populations via larval dispersal is essential for understanding whether populations within reserves replenish those outside (the "seeding effect"). Second, knowledge of the movement patterns of animals into and out of reserves is required to understand whether individuals that settle and grow within reserves eventually move to adjacent unprotected areas, thereby augmenting fisheries (the "spillover effect"). Documenting this phenomenon requires knowledge of home ranges, erratic movements, dispersal,

BOX 7.1. General Research Priorities and Specific Action Items in Marine Conservation Biology

Understanding the Nature of Marine Biodiversity

- *1. Map the distribution of and threats to biodiversity (ecosystems, species, genes).
 - Use geographic information systems to assemble existing data.
 - Determine whether habitat-generating and visually dominant species can provide accurate indices of total biodiversity.
 - Identify regions of high species richness, crucial habitats, special environments, and sensitive ecosystems.
2. Document temporal changes in biodiversity (ecosystems, species) over historical and geological time scales.
 - Examine historical records to document recent changes in ecosystems and biodiversity.
 - Examine paleontological data to estimate background rates of extinction.
3. Explore the ecological mechanisms driving population dynamics, structuring communities, and affecting biodiversity in several key ecosystems.
 - Focus on understanding the ecology of small open-ocean fishes and krill, coastal bottom-oriented fishes, and coral reefs.
 - Determine population boundaries and connectivity, as well as natural mechanisms of population regulation.
 - Determine community-level mechanisms that naturally maintain biodiversity.

Understanding the Threats to Marine Biodiversity

- *1. Document how physical alteration and fragmentation of habitats affect seafloor ecosystems.
 - Determine relationship between habitat loss and species loss.
 - Determine effects of habitat fragmentation on population viability.

and migrations of mobile juveniles and adults, and thus innovations in tagging and telemetry. Third, simultaneous socioeconomic studies are necessary to document feedback between exploited marine populations and human society. Again, such knowledge should be used in the framework of adaptive management after immediate implementation of provisional reserves based on existing data.

- *Develop the science of marine restoration ecology.* Given the high level of degradation already suffered by many coastal ecosystems—especially estuarine salt marshes and mangroves, coral reefs, and seagrass beds—

- *2. Document how overfishing alters marine food webs.
 - Document cascading effects of declining large vertebrates (predatory fishes, sea turtles, seabirds, and marine mammals) on ecosystem function and stability.
 - Explore effects of biomass dominance shifts on ecosystem function and stability.
 - Document effects of discarded bycatch on ecosystem function and stability.
- *3. Document how species introductions affect native species and alter community structure.
 - Determine mechanisms by which introduced exotic species become established and displace native species.
 - Document impacts of exotic disease organisms introduced by human activities.
 - Document effects of genetically modified mariculture species on native species.
- *4. Document how the increasing scale of human-induced eutrophication alters ecosystems.
 - Determine effects of algal blooms and resulting dead zones on biodiversity and ecosystems.

Taking Action to Conserve Marine Biodiversity

- *1. Implement and evaluate networks of marine protected areas.
 - Implement adaptive management to evaluate and optimize siting, number, size, and spacing of reserves.
 - Document ecological changes inside vs. outside reserves and test whether and how populations inside reserves replenish those outside.
- 2. Develop the science of marine restoration ecology.
 - Develop methods to enhance recovery of degraded ecosystems.

Note: Asterisks denote the six highest priorities for the decade.

research on how to augment recovery of these systems will be useful if and when environmental assaults are ameliorated. The science of marine restoration ecology is in its infancy (Thayer 1992; NRC 1994) and focuses mostly on estuarine systems (Kennish 2000; Zedler 2000). Besides controlling deleterious inputs, case studies to date on enhancing recovery include cleanup following oil spills (Doerffer 1992; see also Paine et al. 1996; Peterson 2000), rehabilitation of mangroves (Day et al. 1999), and transplants of corals and seagrass (Rinkevich 1995; Bortone 2000). General issues and research priorities in restoration ecology are reviewed in chapter 11.

Conclusions

Because funding constraints often force prioritization of priorities, box 7.1 indicates what we believe to be the six most important research thrusts needed to conserve marine biodiversity. Importantly, so little is known about all aspects of marine biodiversity and its demise that precautionary action is needed immediately, even before new research initiatives (Ludwig et al. 1993; Costanza et al. 1998). The most prudent precautionary measure is to set aside areas of the oceans for protection from all direct human activities. Establishing substantial networks of no-take marine reserves in an adaptive management framework will allow us to separate the effects of direct and local human impacts (physical alteration of habitat, overexploitation, local species introductions, and point-source pollutants) from indirect and ubiquitous effects (wide-ranging species introductions, global climate change, widespread pollutants), as well as to examine experimentally the most effective size, shape, spacing, and location of reserves (Murray et al. 1999). Additional precautionary action would be to reverse the burden of proof (Dayton 1998), whereby the instigators of potentially deleterious activities would have to demonstrate that their proposed actions are not a threat (rather than the present situation in which environmental regulators have to document that a deleterious effect has occurred). Success of these measures will require environmental scientists to educate the public and policy makers concerning the importance of action despite scientific uncertainty. Fundamental change is needed regarding the role of the scientist-citizen in society so that scientific advocacy is no longer considered an oxymoron (Hixon 2000). Once precautionary policies are implemented, major research efforts are required to effect adaptive management and enlightened conservation efforts that balance the necessity of conserving life in the sea with society's need to exploit marine resources. The risks of continued research without immediate conservation action are too great to ignore.

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LITERATURE CITED

- Agardy, M. T. 1997. *Marine Protected Areas and Ocean Conservation*. San Diego: Academic Press.
- Alverson, D. L., M. H. Freeberg, J. G. Pope, and S. A. Murawski. 1994. *A global assessment of fisheries bycatch and discards*. FAO Fisheries Technical Paper 339. Rome: FAO.
- Aronson, R. B. 1990. Onshore-offshore patterns of human fishing activity. *Palaos* 5: 88–93.
- Auster, P. J., and R. W. Langton. 1999. The effects of fishing on fish habitat. *American Fisheries Society Symposium* 22: 150–187.
- Awise, J. C. 1998. Conservation genetics in the marine realm. *Journal of Heredity* 89: 377–382.
- Bartlett, D., and R. W. G. Carter. 1991. Seascape ecology: The landscape ecology of the coastal zone. *Ecology (CSSR)* 10: 43–53.
- Bohnsack, J., B. Causey, M. Crosby, R. Griffis, M. Hixon, T. Hourigan, K. Koltes, J. Maragos, A. Simons, and J. Tilmant. In review. *A Rationale for a Minimum of 20% No-Take Protection for Coral Reefs*.
- Borque, B. J. 1996. *Diversity and Complexity in Prehistoric Maritime Societies: A Gulf of Maine Perspective*. New York: Plenum Press.
- Bortone, S. A., ed. 2000. *Seagrasses: Monitoring, Ecology, Physiology, and Management*. Boca Raton, Fla: CRC Press.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277: 509–515.
- Briggs, J. C. 1974. *Marine Zoogeography*. New York: McGraw-Hill.
- Burkholder, J. M. 1998. Implications of harmful microalgae and heterotrophic dinoflagellates in management of sustainable marine fisheries. *Ecological Applications*, 8(1) Supplement: S37–S62.
- Butman, C. A., J. T. Carlton, and S. R. Palumbi. 1995. Whaling effects on deep-sea biodiversity. *Conservation Biology* 9: 462–464.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27: 477–500.
- Carlton, J. T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: The biology of ballast water. *Oceanography and Marine Biology Annual Review* 23: 313–371.
- Carlton, J. T. 1993. Neoextinctions of marine invertebrates. *American Zoologist* 33: 499–509.

- Carlton, J. T. 1996. Biological invasions and cryptogenic species. *Ecology* 77: 1653–1655.
- Carlton, J. T. 1999. The scale and ecological consequences of biological invasions in the world's oceans. Pages 195–212 in O. T. Sandlund, P. J. Schei, and Å. Viken, eds., *Invasive Species and Biodiversity Management*. Dordrecht, Netherlands: Kluwer Academic Publishers.
- Carlton, J. T., and J. B. Geller. 1993. Ecological roulette: The global transport of non-indigenous marine organisms. *Science* 261: 78–82.
- Carlton, J. T., J. B. Geller, M. L. Reaka-Kudla, and E. A. Norse. 1999. Historical extinctions in the sea. *Annual Review of Ecology and Systematics* 30: 515–538.
- Carlton, J. T., G. J. Vermeij, D. R. Lindberg, D. A. Carlton, and E. Dudley. 1991. The first historical extinction of a marine invertebrate in an ocean basin: The demise of the eelgrass limpet *Lottia alveus*. *Biological Bulletin* 180: 72–80.
- Casey, J. M., and R. A. Myers. 1998. Near extinction of a large, widely distributed fish. *Science* 281: 690–692.
- Childress, J. J. 1983. Oceanic biology: Lost in space? Pages 127–135 in P. Brewer, ed., *Oceanography: The Present and Future*. New York: Springer-Verlag.
- Chisholm, S. W., R. J. Olson, E. R. Zettler, R. Goericke, J. B. Waterbury, and N. A. Welschmeyer. 1988. A novel free-living prochlorophyte abundant in the oceanic euphotic zone. *Nature* 334: 340–343.
- Cohen, J. E. 1994. Marine and continental food webs: Three paradoxes? *Philosophical Transactions of the Royal Society, Series B* 343: 57–69.
- Coleman, F. C., C. C. Koenig, and C. B. Grimes. 2000. Long-lived reef fishes: The grouper-snapper complex. *Fisheries* 25(3): 14–21.
- Corliss, J. O. 1994. An interim utilitarian (“user friendly”) hierarchical classification and characterization of the protists. *Acta Protozoologica* 33: 1–51.
- Costanza, R. 1999. The ecological, economic, and social importance of the oceans. *Ecological Economics* 31: 199–213.
- Costanza, R., F. Andrade, P. Antunes, M. van den Belt, D. Boersma, D. F. Boesch, F. Catarino, S. Hanna, L. Limburg, B. Low, M. Molitor, J. G. Pereira, S. Rayner, R. Santos, J. Wilson, and M. Young. 1998. Principles for sustainable governance of the oceans. *Science* 281: 198–199.
- Costanza, R., F. Andrade, P. Antunes, M. van den Belt, D. Boesch, D. Boersma, F. Catarino, S. Hanna, L. Limburg, B. Low, M. Molitor, J. G. Pereira, S. Rayner, R. Santos, J. Wilson, and M. Young. 1999. Ecological economics and sustainable governance of the oceans. *Ecological Economics* 31: 171–187.
- Costanza, R., R. d’Arge, R. d. Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O’Neill, J. Paruelo, R. G. Raskin, P. Sutton, and M. van den Belt. 1997. The value of the world’s ecosystem services and natural capital. *Nature* 387: 253–260.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* 14: 405–410.
- Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: Open or closed? *Science* 287: 857–859.

- Crowder, L. B., and S. A. Murawski. 1998. Fisheries bycatch: Implications for management. *Fisheries* 23(6): 8–17.
- Culotta, E. 1994. Is marine biodiversity at risk? *Science* 263: 918–920.
- Cushing, D. 1995. *Population production and regulation in the sea: A fisheries perspective*. Cambridge, U.K.: Cambridge University Press.
- Daily, G. C., ed. 1997. *Nature's Services*. Washington, D.C.: Island Press.
- Day, S., W. J. Streever, and J. J. Watts. 1999. An experimental assessment of slag as a substrate for mangrove rehabilitation. *Restoration Ecology* 7: 139–144.
- Dayton, P. K. 1998. Reversal of the burden of proof in fisheries management. *Science* 279: 821–822.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* 8: 309–322.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5: 205–232.
- Diaz, R. J., and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology Annual Review* 33: 245–303.
- Doerffer, J. W., ed. 1992. *Oil Spill Response in the Marine Environment*. Oxford, U.K.: Pergamon Press.
- Earll, R. C. 1992. Commonsense and the precautionary principle: An environmentalist's perspective. *Marine Pollution Bulletin* 24: 182–186.
- Elmgren, R. 1989. Man's impact on the ecosystem of the Baltic Sea: Energy flows today and at the turn of the century. *Ambio* 18: 326–332.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking coastal with oceanic ecosystems. *Science* 282: 473–476.
- FAO. 1997. *Review of the State of World Fishery Resources: Marine Fisheries*. FAO Fisheries Circular 920. Rome: FAO.
- Feldmann, R. M., and R. B. Manning. 1992. Crisis in systematic biology in the "Age of Biodiversity." *Journal of Paleontology* 66: 157–158.
- Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. *Science* 281: 237–240.
- Fogarty, M. J., and S. A. Murawski. 1998. Large-scale disturbance and the structure of marine ecosystems: Fishery impacts on Georges Bank. *Ecological Applications* 8(1) Supplement: S6–S22.
- Fortes, M. D. 1988. Mangrove and seagrass beds of East Asia: Habitats under stress. *Ambio* 17: 207–213.
- Fuhrman, J. A. 1999. Marine viruses and their biogeochemical and ecological effects. *Nature* 399: 541–548.
- GESAMP. 1990. *The State of the Marine Environment*. Oxford, U.K.: Blackwell Scientific Publications.

- Giovannoni, S. J., T. B. Britschgi, C. L. Moyer, and K. G. Field. 1990. Genetic diversity in Sargasso Sea bacterioplankton. *Nature* 345: 60–63.
- Grassle, J. F., P. Lasserre, A. D. McIntyre, and G. C. Ray. 1991. Marine biodiversity and ecosystem function: A proposal for an international programme of research. *Biology International* (Special Issue) 23: 1–19.
- Grassle, J. F., and N. J. Maciolek. 1992. Deep-sea species richness: Regional and local diversity estimates from quantitative bottom samples. *American Naturalist* 139: 313–341.
- Griffis, R. B., and K. W. Kimball. 1996. Ecosystem approaches to coastal and ocean stewardship. *Ecological Applications* 6: 708–712.
- Hall, M. A. 1996. On bycatches. *Reviews in Fish Biology and Fisheries* 6: 319–352.
- Hall, S. J. 1999. *The Effects of Fishing on Ecosystems and Communities*. Oxford, U.K.: Blackwell Science.
- Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase. *Phycologia* 32: 79–99.
- Harvell, C. D., K. Kim, J. M. Burkholder, R. R. Colwell, P. R. Epstein, D. J. Grimes, E. E. Hofmann, E. K. Lipp, A. D. M. E. Osterhaus, R. M. Overstreet, J. W. Porter, G. W. Smith, and G. R. Vasta. 1999. Emerging marine diseases—Climate links and anthropogenic factors. *Science* 285: 1505–1510.
- Hixon, M. A. 2000. Environmental advocacy: Dilemma of the citizen-scientist. *Reflections* Special Issue 4: 13.
- Hixon, M. A., and M. S. Webster. 2001. Density dependence in marine fishes: Coral-reef populations as model systems. In P. F. Sale, ed., *Advances in the Ecology of Fishes on Coral Reefs*. San Diego: Academic Press.
- Holling, C. S. 1978. *Adaptive Environmental Assessment and Management*. New York: John Wiley and Sons.
- Hughes, T. P. 1994. Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547–1551.
- Huston, M. A., ed. 1994. *Species Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge, U.K.: Cambridge University Press.
- Irish, K. E., and E. A. Norse. 1996. Scant emphasis on marine biodiversity. *Conservation Biology* 10: 680.
- Irlandi, E. A., and M. K. Crawford. 1997. Habitat linkages: The effect of subtidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110: 231–236.
- Jackson, J. B. C. 1995. Constancy and change of life in the sea. Pages 45–54 in J. H. Lawton and R. M. May, eds., *Extinction Rates*. Oxford, U.K.: Oxford University Press.
- Jackson, J. B. C. 1997. Reefs since Columbus. *Coral Reefs* 16 (supplement): S23–S32.
- Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. *Advances in Marine Biology* 34: 201–352.
- Johannes, R. E. 1981. *Words of the Lagoon: Fishing and Marine Lore in the Palau District of Micronesia*. Berkeley: University of California Press.
- Johannes, R. E. 1998. The case for data-less marine resource management: Examples from tropical nearshore finfisheries. *Trends in Ecology and Evolution* 13: 243–246.

- Johannes, R. E., and M. Riepen. 1995. *Environmental, Economic and Social Implications of the Live Reef Fish Trade in Asia and the Western Pacific*. Jakarta, Indonesia: The Nature Conservancy.
- Johnston, C. A. 1998. *GIS: In ecology*. Oxford, U.K.: Blackwell.
- Jones, J. B. 1992. Environmental impact of trawling on the seabed: A review. *New Zealand Journal of Marine and Freshwater Research* 26: 59–67.
- Jones, G. P., and N. L. Andrew. 1993. Temperate reefs and the scope of seascape ecology. Pages 63–76 in C. N. Battershill, D. R. Schiel, G. P. Jones, R. G. Creese, and A. B. MacDiarmid, eds., *Proceedings of the Second International Temperate Reef Symposium*. NIWA Marine, Wellington, New Zealand.
- Jones, G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. *Nature* 402: 802–804.
- Kaly, U. L., and G. P. Jones. 1998. Mangrove restoration: A potential tool for coastal management in tropical developing countries. *Ambio* 27: 656–661.
- Kennish, M. J. 1998. *Pollution Impacts on Marine Biotic Communities*. Boca Raton, Fla.: CRC Press.
- Kennish, M. J., ed. 2000. *Estuary Restoration and Maintenance: The National Estuary Program*. Boca Raton, Fla.: CRC Press.
- Knowlton, N. 1993. Sibling species in the sea. *Annual Review of Ecology and Systematics* 24: 189–216.
- Leslie, H., M. Ruckelshaus, I. Ball, H. Possingham, and S. Andelman. In press. *Using Siting Algorithms in the Design of Marine Reserve Networks*.
- Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? *Annual Review of Ecology and Systematics* 19: 371–393.
- Lichtatowich, J. A., G. R. Guido, S. M. Whidden, and C. R. Steward. 2000. Sanctuaries for Pacific salmon. Pages 675–686 in E. E. Knudsen, C. R. Steward, D. D. MacDonald, J. E. Williams, and D. W. Reiser, eds., *Sustainable Fisheries Management: Pacific Salmon*. Boca Raton, Fla.: Lewis Publishers.
- Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal, and P. G. Risser. 1991. The sustainable biosphere initiative: An ecological research agenda. *Ecology* 72: 371–412.
- Ludwig, D., R. Hilborn, and C. Walters. 1993. Uncertainty, resource exploitation, and conservation: Lessons from history. *Science* 260: 17, 36.
- Malakoff, D. 1997. Extinction on the high seas. *Science* 277: 486–488.
- Maragos, J. E., M. P. Crosby, and J. W. McManus. 1996. Coral reefs and biodiversity: A critical and threatened relationship. *Oceanography* 9: 83–99.
- Marx, W. 1999. *The Frail Ocean*. Point Roberts, Wash.: Hartley and Marks Publishers.
- May, R. M. 1994. Biological diversity: Differences between land and sea. *Philosophical Transactions of the Royal Society*, Series B 343: 105–111.
- May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt, and R. M. Laws. 1979. Management of multispecies fisheries. *Science* 205: 267–277.
- McAllister, D. E. 1996. *The Status of the World Ocean and Its Biodiversity*. Ottawa, Canada: Ocean Voice International.

- Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic systems. *Science* 285: 1396–1398.
- Micheli, F., and C. H. Peterson. 1999. Estuarine vegetated habitats as corridors for predator movements. *Conservation Biology* 13: 869–881.
- Moberg, F., and C. Folke. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29: 215–233.
- Murray, S. N., R. F. Ambrose, J. A. Bohnsack, L. W. Botsford, M. H. Carr, G. E. Davis, P. K. Dayton, D. Gotshall, D. R. Gunderson, M. A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D. A. McArdle, J. C. Ogden, J. Roughgarden, R. M. Starr, M. J. Tegner, and M. M. Yoklavich. 1999. No-take reserve networks: Protection for fishery populations and marine ecosystems. *Fisheries* 24: 11–25.
- Musick, J. A., S. A. Berkeley, G. M. Cailliet, M. Camhi, G. Huntsman, M. Nammack, and M. L. Warren Jr. 2000. Protection of marine fish stocks at risk of extinction. *Fisheries* 25(3): 6–8.
- Musick, J. A., G. Burgess, G. Cailliet, M. Camhi, and S. Fordham. 2000. Management of sharks and their relatives (Elasmobranchii). *Fisheries* 25(3): 9–13.
- Myers, N., and J. Kent. 1998. *Perverse Subsidies: Tax \$s Undercutting Our Economies and Environments Alike*. Winnipeg, Canada: International Institute for Sustainable Development.
- Naylor, R. L., R. J. Goldberg, J. H. Primavera, N. Kautsky, M. C. M. Beveridge, J. Clay, C. Folke, J. Lubchenco, H. Mooney, and M. Troell. 2000. Effect of aquaculture on world fish supplies. *Nature* 405: 1071–1024.
- Nelson, W. G. 1993. Beach restoration in the southeastern U.S.: Environmental effects and biological monitoring. *Ocean Coastal Management* 19: 157–182.
- Norse, E. A., ed. 1993. *Global Marine Biological Diversity: A Strategy for Building Conservation into Decision Making*. Washington, D.C.: Island Press.
- NRC (National Research Council). 1994. *Restoring and Protecting Marine Habitat: The Role of Engineering and Technology*. Washington, D.C.: National Academy Press.
- NRC (National Research Council). 1995. *Understanding Marine Biodiversity: A Research Agenda for the Nation*. Washington, D.C.: National Academy Press.
- NRC (National Research Council). 1998. *Improving Stock Assessments*. Washington, D.C.: National Academy Press.
- NRC (National Research Council). 1999. *Sustaining Marine Fisheries*. Washington, D.C.: National Academy Press.
- Ogden, J. C., and E. H. Gladfelter, eds. 1986. *Caribbean Coastal Marine Productivity*. Paris: UNESCO.
- Olson, R. J., S. W. Chisholm, E. R. Zettler, M. Altabet, and J. Dusenberry. 1990. Spatial and temporal distributions of prochlorophyte picoplankton in the North Atlantic Ocean. *Deep-Sea Research II* 37: 1033–1051.
- Ormond, R. F. G., J. D. Gage, and M. V. Angel, eds. 1997. *Marine Biodiversity: Patterns and Processes*. Cambridge, U.K.: Cambridge University Press.

- Paine, R. T., J. L. Ruesink, A. Supp, E. L. Soulanille, M. J. Wonham, C. D. G. Harley, D. R. Brumbaugh, and D. L. Secord. 1996. Trouble on oiled waters: Lessons from the *Exxon Valdez* oil spill. *Annual Review of Ecology and Systematics* 27: 197–235.
- Palumbi, S. R. 1992. Marine speciation on a small planet. *Trends in Ecology and Evolution* 7: 114–118.
- Palumbi, S. R. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* 25: 547–572.
- Palumbi, S. R. 2001. The ecology of marine protected areas. In M. D. Bertness, S. D. Gaines, and M. E. Hay, eds., *Marine Community Ecology*, pp. 509–530. Sunderland, Mass.: Sinauer Associates.
- Pandolfi, J. M., and P. R. Minchin. 1995. A comparison of taxonomic composition and diversity between reef coral life and dead assemblages in Madang Lagoon, Papua New Guinea. *Palaeogeography Palaeoclimatology Palaeoecology* 119: 321–341.
- Pandolfi, J. M., and J. B. C. Jackson. 2001. Community structure of Pleistocene coral reefs of Curaçao, Netherlands Antilles. *Ecological Monographs* 71: 49–67.
- Parker, S. J., S. A. Berkeley, J. T. Golden, D. R. Gunderson, J. Heifetz, M. A. Hixon, R. Larson, B. M. Leaman, M. S. Love, J. A. Musick, V. M. O'Connell, S. Ralston, H. J. Weeks, and M. M. Yoklavich. 2000. Management of Pacific rockfish. *Fisheries* 25(3): 22–30.
- Pauly, D. 1988. Some definitions of overfishing relevant to coastal zone management in southeast Asia. *Tropical Coastal Area Management* 3: 14–15.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends in Ecology and Evolution* 10: 430.
- Pauly, D., and V. Christensen. 1995. Primary production required to sustain global fisheries. *Nature* 374: 255–257.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr. 1998. Fishing down marine food webs. *Science* 279: 860–863.
- Peterson, C. H. 2001. The *Exxon Valdez* oil spill in Alaska: Acute, indirect, and chronic effects on the ecosystem. *Advances in Marine Biology* 39: 1–103.
- Peterson, C. H., and J. A. Estes. 2001. Conservation and management of marine communities. Pages 469–507 in M. D. Bertness, S. D. Gaines, and M. E. Hay, eds., *Marine Community Ecology*. Sunderland, Mass.: Sinauer Associates.
- Peterson, C. H., D. H. M. Hickerson, and G. G. Johnson. 2000. Short-term consequences of nourishment and bulldozing on the dominant large invertebrates of a sandy beach. *Journal of Coastal Research* 16: 368–378.
- Peterson, M. N. A., ed. 1992. *Diversity of Oceanic Life: An Evaluative Review*. Washington, D.C.: Center for Strategic and International Studies.
- Pickett, S., R. S. Ostfeld, M. Shachak, and G. E. Likens, eds. 1998. *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity*. Hingham, Mass.: Kluwer Academic Publishers.
- Ray, G. C. 1991. Coastal-zone biodiversity patterns. *BioScience* 41: 490–498.
- Ray, G. C. 1996. Coastal-marine discontinuities and synergisms: Implications for biodiversity conservation. *Biodiversity and Conservation* 5: 1095–1108.

- Ray, G. C. 1999. Coastal-marine protected areas: Agonies of choice. *Aquatic Conservation: Marine and Freshwater Ecosystems* 9: 607–614.
- Ray, G. C., and B. P. Hayden. 1992. Coastal zone ecotones. Pages 403–420 in A. J. Hansen and F. D. Castri, eds., *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. New York: Springer-Verlag.
- Reaka-Kudla, M. L. 1997. The global biodiversity of coral reefs: A comparison with rainforests. Pages 83–108 in M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, eds., *Biodiversity II: Understanding and Protecting Our Biological Resources*. Washington, D.C.: National Academy Press.
- Rinkevich, B. 1995. Restoration strategies for coral reefs damaged by recreational activities: Use of sexual and asexual recruits. *Restoration Ecology* 3: 241–251.
- Roberts, C. M., and J. P. Hawkins. 1999. Extinction risk in the sea. *Trends in Ecology and Evolution* 14: 241–246.
- Roberts, C. M., J. P. Hawkins, D. E. McAllister, and F. W. Schueler. 2001. Hotspots, endemism and the conservation of coral reef fish biodiversity. *Coral Reefs*, in press.
- Rothschild, B. J. 1986. *Dynamics of Marine Fish Populations*. Cambridge, Mass.: Harvard University Press.
- Ruiz, G. M., J. T. Carlton, E. D. Grosholz, and A. H. Hines. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: Mechanisms, extent, and consequences. *American Zoologist* 37: 621–632.
- Ruiz, G. M., P. Fofonoff, and A. H. Hines. 1999. Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. *Limnology and Oceanography* 44: 950–972.
- Ryman, N. 1991. Conservation genetics considerations in fishery management. *Journal of Fish Biology* 39: 211–234.
- Safina, C. 1995. The world's imperiled fish. *Scientific American* 273: 46–53.
- Sale, P. F., ed. 1991. *The Ecology of Fishes on Coral Reefs*. San Diego: Academic Press.
- Schlesinger, W. H. 1997. *Biogeochemistry: An Analysis of Global Change*. San Diego: Academic Press.
- Sepkoski, J. J. 1992. Phylogenetic and ecologic patterns in the Phanerozoic history of marine biodiversity. Pages 77–100 in N. Eldredge, ed., *Systematics, Ecology, and the Biodiversity Crisis*. New York: Columbia University Press.
- Sheppard, C. 1995. The shifting baseline syndrome. *Marine Pollution Bulletin* 30: 766–767.
- Sherman, K., L. M. Alexander, and B. D. Gold, eds. 1990. *Large Marine Ecosystems: Patterns, Processes, and Yields*. Washington, D.C.: American Association for the Advancement of Science.
- Simenstad, C. A., J. A. Estes, and K. W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science* 200: 403–410.
- Sindermann, C. J. 1996. *Ocean Pollution: Effects on Living Resources and Humans*. Boca Raton, Fla.: CRC Press.
- Smith, P. J., R. I. C. C. Francis, and M. McVeagh. 1991. Loss of genetic diversity due to fishing pressure. *Fisheries Research* 10: 309–316.
- Snelgrove, V. R., T. H. Blackburn, P. A. Hutchings, D. M. Alongi, J. F. Grassle, H. Hummel, G. King, I. Koike, P. J. D. Lamshead, N. B. Ramsing, and V. Solis-

- Weiss. 1997. The importance of marine sediment biodiversity in ecosystem processes. *Ambio* 26: 578–583.
- Soulé, M. E., ed. 1987. *Viable Populations for Conservation*. Cambridge, U.K.: Cambridge University Press.
- Steele, J. H. 1974. *The Structure of Marine Ecosystems*. Cambridge, Mass.: Harvard University Press.
- Steele, J. H. 1985. A comparison of terrestrial and marine ecological systems. *Nature* 313: 355–358.
- Steneck, R. S., and J. T. Carlton. 2001. Human alterations of marine communities: Students beware! *Caveat studium*. Pages 445–468 in M. D. Bertness, S. D. Gaines, and M. E. Hay, eds., *Marine Community Ecology*. Sunderland, Mass.: Sinauer Associates.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. *Nature* 402: 799–802.
- Tegner, M. J., L. V. Basch, and P. K. Dayton. 1996. Near extinction of an exploited marine invertebrate. *Trends in Ecology and Evolution* 11: 278–280.
- Thayer, G. W., ed. 1992. *Restoring the Nation's Marine Environment*. College Park, Md.: Maryland Sea Grant.
- Thorne-Miller, B. 1999. *The Living Ocean: Understanding and Protecting Marine Biodiversity*. Washington, D.C.: Island Press.
- Tunnicliffe, V. 1991. The biology of hydrothermal vents: Ecology and evolution. *Oceanography and Marine Biology Annual Review* 29: 319–407.
- Turner, R. E., and N. N. Rabalais. 1994. Coastal eutrophication near the Mississippi River delta. *Nature* 368: 619–621.
- Van Dover, C. L. 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton, N.J.: Princeton University Press.
- Vecchione, M., and B. B. Collette. 1996. The central role of systematics in marine biodiversity problems. *Oceanography* 9: 44–45.
- Vermeij, G. J. 1993. Biogeography of recently extinct marine species: Implications for conservation. *Conservation Biology* 7: 391–397.
- Vincent, A. C. J., and H. J. Hall. 1996. The threatened status of marine fishes. *Trends in Ecology and Evolution* 11: 360–361.
- Vitousek, P. M., H. A. Moones, J. Lubchenco, and J. M. Melillo. 1997. Human domination of the earth's ecosystems. *Science* 277: 494–499.
- Walters, C. J., and R. Hilborn. 1978. Ecological optimization and adaptive management. *Annual Review of Ecology and Systematics* 9: 157–188.
- Ward, T. J., M. A. Vanderklift, A. O. Nicholls, and R. A. Kenchington. 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications* 9: 691–698.
- Watling, L., and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conservation Biology* 12: 1180–1197.
- WCMC. 1992. *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman and Hall.
- Wilkinson, C. R. 1999. Global and local threats to coral reef functioning and existence: Review and predictions. *Marine and Freshwater Research* 50: 867–878.

- Winston, J. E. 1992. Systematics and marine conservation. Pages 144–168 in N. Eldredge, ed., *Systematics, Ecology, and the Biodiversity Crisis*. New York: Columbia University Press.
- Woodard, C. 2000. *Ocean's End: Travels through Endangered Seas*. New York: Basic Books.
- Zaitsev, Y. 1992. Recent changes in the trophic structure of the Black Sea. *Oceanography* 1: 180–189.
- Zedler, J. B., ed. 2000. *Handbook for Restoring Tidal Wetlands*. Boca Raton, Fla.: CRC Press.

CONSERVATION BIOLOGY AND THE HEALTH SCIENCES

Defining the Research Priorities of Conservation Medicine

Gary M. Tabor, Richard S. Ostfeld, Mary Poss,
Andrew P. Dobson, and A. Alonso Aguirre

Human impacts on the health of the planet can be characterized within four areas of environmental concern (Colborn et al. 1993; Colborn et al. 1996; Rees 1996; Wilson 1988; Woodwell and Houghton 1990):

1. increasing biological impoverishment, which includes the loss of biodiversity and modification of ecological processes;
2. increasing global "toxification," which includes the spread of hazardous wastes and toxic substances and the impact of endocrine-disrupting hormones;
3. global climate change and ozone depletion; and
4. an increasing human "ecological footprint" as a result of our exponentially growing population and use of resources (an ecological footprint is an area-based calculation used in environmental economics to determine human impacts on natural resources).

The discreet and cumulative impacts of these human-induced global changes not only have diminished the environmental capital of the planet but also have yielded an array of health concerns, including the increasing spread of infectious (e.g., malaria) and noninfectious (e.g., melanoma) diseases, and the

growing physiological impacts on species' reproductive health, developmental biology, and immune system response (e.g., endocrine disruptors) (Blaustein et al. 1994; Blaustein and Wake 1995; Colborn et al. 1996; Lurance et al. 1996; Epstein 1995; McMichael and Haines 1997; Patz et al. 1996).

The ecological impacts of humans can ripple throughout ecological communities. The demise of one species, or the rise of one species at the expense of another, may establish a trophic cascade of ecological responses (see chapter 3). When predator-prey or species competition relationships are disrupted, ecological impacts may extend beyond the predator and prey or the competitors (Estes et al. 1998; Epstein et al. 1997; Pace et al. 1999; Ostfeld and Keesing 2000b). The spread of Lyme disease as a result of the changing ecology of white-tailed deer (*Odocoileus virginianus*) and white-footed mice (*Peromyscus leucopus*) in a landscape devoid of large predators and diminished biodiversity is a good example of ecological magnification of disease (Ostfeld and Keesing 2000a).

Certainly global climate change adds to the complexity of disease impacts in conservation. This issue is one of the most pressing ecological health concerns. For instance, global climate change may impact health by promoting the spread of infectious disease from more tropical ranges to temperate areas, expanding beyond latitudinal and altitudinal zones. This phenomenon may be apparent in diseases such as malaria and dengue fever (Epstein 1995, 1997; Patz et al. 1996; Rogers and Randolph 2000). The potential impact of climate change on ecological processes may be profound: increased precipitation in some regions and drought in others; increased erosion of the coastal zone with rising sea levels; and the inability of many species to adapt to the relatively rapid changes in climatic regimes, potentially resulting in mass extinctions (Epstein 1999; McMichael 1997; McMichael et al. 1999). Changes in atmospheric volatilization and deposition of pollutants also are of concern as warmer temperatures and greater precipitation enhance pollutant transport (Blais et al. 1998; Schindler 1999).

Since its origin, conservation biology has understood the implications of health and disease in management of species and habitat. The integration of theory into practice is only recently emerging with the rise of the new field of conservation medicine (Frankel and Soule 1981; Dobson and May 1986; Grenfell and Dobson 1995; Meffe 1999; Pokras et al. 1999). Understanding the ecological aspects of health and disease is a future challenge for conservation biologists, who are increasingly expected to provide management remedies for ecological health concerns.

Conservation Medicine: A Brief Description

Conservation biology and conservation medicine have the common aim of trying to achieve ecological health. Conservation medicine studies the two-

way interactions between pathogens and disease on the one hand, and species and ecosystems on the other. It focuses on the study of the ecological context of health and the remediation of ecological health problems. In response to the growing health implications of environmental degradation, conservation medicine has emerged as a new interdisciplinary field to address the complex interrelationship between health and ecological concerns. As such, conservation medicine's purview includes examining the linkages among (1) changes in habitat structure and land use; (2) emergence and reemergence of infectious agents, parasites, and environmental contaminants; and (3) maintenance of biodiversity and ecosystem functions as they sustain the health of plant and animal communities including humans. For example, conservation medicine is concerned with the effects of disease on rare or endangered species and on the functioning of ecosystems. It is also concerned with the impacts of changes in species diversity or rarity on disease maintenance and transmission.

The dynamic balance that we term health is conceptualized using a set of widely varying spatial scales by many disciplines including human medicine, public health, epidemiology, veterinary medicine, toxicology, ecology, and conservation biology. Conservation medicine represents an approach that bridges those disciplines to examine the health of individuals, groups of individuals, and the landscapes in which they live as an indivisible continuum (Meffe 1999; Pokras et al. 1999).

Conservation medicine, like other interdisciplinary approaches, brings together scientific disciplines "long separated by academic and practical tradition" (Wilson 1992). By reaching out to multiple disciplines, conservation medicine provides new skills, tools, and vision to the fields of both conservation biology and medicine. This includes bringing biomedical research and diagnostic resources to address conservation problems such as development of new noninvasive health monitoring techniques; training health professionals and conservation biologists in the promotion and practice of ecological health; and establishing interdisciplinary teams of health and ecological professionals to assess and redress ecological health problems.

Why Should Conservation Biologists Care about Disease?

Pathogens and infectious diseases create special problems for both the protection of endangered species and the maintenance of biodiversity. In several cases the introduction of a pathogen has produced a significant further decline in the numbers of an already endangered species: canine distemper in black-footed ferrets (*Mustela nigripes*) (Thorne and Williams 1988; Williams et al. 1988); rabies and canine distemper in hunting dogs (*Lycaon pictus*) in Serengeti (Dye 1996; Ginsberg et al. 1995; Heinsohn 1992); and avian malaria in endemic Hawaiian birds (Warner 1968; van Riper III et al. 1986). In all of

these examples, the pathogens involved utilized common or domestic species as reservoir hosts. There is increasing evidence that species diversity may provide an important buffer that minimizes the impact of a pathogen on a population. Paradoxically, pathogens may also play a role in both maintaining biodiversity and driving processes that lead to increases in local diversity (Augsburger 1984; Gilbert 1995; Gilbert et al. 1995; Van der Putten and Van der Stoel 1998; Van der Putten et al. 1993).

While increased species diversity may affect the ability of a pathogen to "find" a susceptible host (especially if the pathogen utilizes multiple hosts), many pathogens are so species specific that only the density of a population affects their ability to cause disease. And thus, any sudden change in population demographics and proportion of susceptible hosts within a population can alter pathogen distribution (Aguirre, Hansen, et al. 1995). This density-dependent phenomenon can be demonstrated in various management practices, such as translocations; reintroductions; the creation of feeding stations in winter that bring animals into close contact, such as the National Elk Refuge in Wyoming; and the alteration of traditional migratory corridors that may bring wildlife into closer contact with domestic animals—all of which can facilitate disease spread (Aguirre, Starkey, et al. 1995). Many activities used to manage wildlife populations have the potential to alter pathogen transmission patterns, and conservation biologists need to be mindful of the consequences. To understand disease threats to wildlife populations, some level of basic disease ecology is required. Conservation biologists need to know what pathogens are endemic and use that information to assess and remedy the introduction of exotic pathogens into a population (Aguirre and Starkey, 1994).

Three topics are central to our understanding of the role pathogens play in conservation biology:

1. What roles do relative abundance, susceptibility, and overlap in spatial distribution play in determining rates of pathogen transmission in populations of vulnerable or endangered species? In pathogens that utilize a range of host species, how do these features contribute to cross-species (inter-specific) transmission? More precisely, does ecological information on the behavior and spatial distribution of potential host species complement epidemiological data and allow us to identify species that are most likely to act as reservoir hosts for pathogens that provide a significant threat to rare or endangered species?
2. What are the dynamics of a recently introduced pathogen into a population? In particular, how do deterministic and stochastic factors interact to determine the persistence and extinction of pathogens in populations? Significantly, how are the dynamics affected if the population is small? How do different types of

pathogens contribute to further declines in the abundance of potentially endangered host species?

3. Does the local diversity of species used by a pathogen tend to buffer or increase either its persistence or rate of spread? Can a pathogen alter the diversity of species that coexist in any community?

Central to all of these problems is the development of a quantitative understanding of how pathogens affect the dynamics of communities that contain one or more potential host species. Here we need to develop empirical and theoretical analyses that examine the role that pathogens play in mediating the coexistence of potentially competing species or in maintaining genetic diversity within a single host species. *We then need to examine whether the diversity of host species tends to either buffer or amplify disease outbreaks.* This is probably the central question in understanding the role that pathogens play in conservation biology. It has very practical applications in conservation, because many proposed management strategies are based on the rationale that biological diversity leads to greater resilience (Pimm 1984; Schulze and Mooney 1994; Hollings et al. 1995).

Determining the answers will require the exploration of the ecological interactions between mode of transmission, host diversity, and pathogen persistence. This can be performed only by examination of empirical data for a number of systems in which we can dissect the relative roles played by host abundance, host resource utilization, and host spatial distribution in determining rates of intra- and interspecific transmission.

In conjunction with these largely deterministic and analytical exercises, we also need to understand the population dynamics of epidemic outbreaks in small (endangered) populations. These analyses will eventually allow the development of stochastic models that determine the impact of pathogens on populations that are too small to sustain a long-term persistent source of infection. Here we also need to focus on examining the costs and benefits of intervention to prevent further spread of the disease, particularly in the limiting case where small host population size always leads to the eventual extinction of the pathogen.

Understanding the Ecology of Disease: An Essential Guide for Conservation Biologists

Pathogens, also known as infectious agents, include viruses, bacteria, fungi, protozoans, and helminths. They undergo population fluctuations within hosts; they compete with one another for access to resources, such as cells and nutrients within hosts; they are preyed upon by host immune agents; they select habitats (tissues); and they disperse within and among hosts. For those

pathogens that are zoonotic (i.e., those that reside within nonhuman vertebrate animals and are transmitted to humans), and those that are transmitted by vectors, ecological interactions are even more complex. Such pathogens must contend with differing environmental conditions within human hosts, nonhuman hosts, and vectors. In addition, the vertebrate hosts and arthropod vectors are involved in complex ecological interactions of their own that will influence the maintenance and transmission of pathogens.

An example of an emerging infectious disease with strong implications for conservation medicine is the 1999–2000 “outbreak” of West Nile virus (WNV) in the northeastern United States (Lanciotti et al. 1999). This mosquito-borne disease, endemic to Europe, Africa, and the Middle East, appeared suddenly in birds and humans in and near New York City and elicited a response by public officials that included extensive aerial spraying of insecticides in densely populated areas. This remedial action, which may be more dangerous to public health and wildlife than the disease itself, and ineffective in reducing disease incidence, was implemented despite our ignorance about the ecology of the mosquito vectors, bird reservoirs, and the pathogen.

For a disease such as this, that has achieved almost daily attention from the mass media, our level of ignorance of the risk and its ecological causes is astonishing. Questions to which no thorough answer exists include: How did WNV disperse to the Western Hemisphere, or was it here all along? Which species function as reservoir hosts (i.e., those from which the mosquito vectors obtain the pathogen)? In which species is the virus pathogenic or lethal, and how does infection influence population dynamics of those species? Over what area does WNV occur, and how does it get there? How do patterns of temperature and rainfall influence breeding performance and populations of container-breeding mosquitoes in urban and suburban ecosystems? Can WNV exist in mosquitoes other than *Culex pipiens* and *Aedes japonicus*? How does the pathogen overwinter? Does it migrate south or stay dormant during the cold winter months (Aguirre et al. 1992)?

Several general principles relevant to conservation medicine are represented by the WNV example. First, in the absence of information on the ecological determinants of disease risk, as well as on the magnitude of that risk, environmentally destructive but largely ineffective measures (e.g., adulticide spraying) are unfortunately employed. Ecological knowledge about zoonoses can help prevent uninformed decision making. Second, environmentally more benign solutions to the WNV problem may require a solid scientific understanding of the roles played by specific bird or mammal reservoirs, diversity in the community of reservoirs, and landscapes that influence diver-

sity. Third, a likely cause of the transoceanic dispersal of the virus is either via movements by people or by domesticated or wild animals (Rappole et al. 2000). Long-distance movements by pathogens such as WNV may represent instances of invasion by exotic species and, therefore, are relevant to both conservation biologists and health scientists. Fourth, some evidence suggests that the container-breeding mosquitoes that carry arthropod-borne viruses become particularly abundant when hot, dry weather prevents flushing of urban pools of water, such as storm drains. Climatic factors may influence disease transmission in unexpected ways (Reisen et al. 1992; Hubalek and Halouzka 1999).

Ecological research can help us anticipate and ameliorate the adverse effects of infectious diseases on humans, domestic animals, and wildlife. From an ecological framework, these infectious diseases occur when a pathogen population disperses to a host, invades, and, via infection, triggers a host immune response resulting in clinical signs. The key elements to which ecological research can contribute is an understanding of where pathogens are maintained in nature, how they disperse to the focal population, and what environmental processes are involved in the maintenance of the pathogen within populations and in transmission among them. Armed with such knowledge, conservation managers may be able to intervene in natural systems to reduce the likelihood of exposure. In box 8.1, we have listed potential research priorities, posed as questions, together with a brief rationale, that link disease, ecology, and conservation biology.

Connecting Pathobiology to Ecology

Investigation of disease and disease pathogenesis is based primarily on studies in domestic animals. However, it may not be accurate to assume that principles developed by studies in domesticated animals will apply to wildlife. Even within the same species, extrapolation across animals from a range of different habitats may be problematic. This is because many infectious agents endemic to a population are adapted to the population structure of their hosts. Dynamics and structure of a host population determine the nature of its microbiologic fauna. Isolated or small populations may maintain different types of pathogens than large and contiguous populations that freely exchange individuals. Because both the genetics of the pathogen and the host environment determine the outcome of infection, it is plausible that in isolated populations, genetic bottlenecking of both host and pathogen may lead to a unique outcome of infection. Thus, although detailed pathogen-host studies provide suitable information, and frequently the only baseline information available, the potential for unique pathogenic outcomes in wildlife species should be considered.

A primary objective should be to determine the extent to which disease caused by endemic microbes can influence survival or fecundity of individuals in a population. Endemic diseases are infrequently considered as factors affecting population survival. Yet infections with endemic organisms may more commonly lead to chronic conditions affecting an animal's ability to forage or escape predators than directly to high mortality. In addition, disease induced by infectious organisms common to a population may have a more profound effect on specific age-classes such as neonates or old adults.

Whereas many pathogens are fastidiously host specific, others, such as canine distemper (family Paramyxoviridae, genus *Morbillivirus*), may be transmitted across species boundaries. Wildlife may also acquire a foreign pathogen from their domesticated counterparts. A significant level of mortality can occur if an exotic pathogenic microorganism is introduced into a naive susceptible population (Anderson 1995; Roelke-Parker et al. 1996). Mathematical models based on dynamics and structure of the susceptible species, and on pathogenic processes and transmission properties of the pathogen, are invaluable in assessing risk of introduced pathogens to host population survival.

In general, infectious agents are relatively easy to identify genetically and serologically. Many diagnostic laboratory techniques are available for assisting conservation biologists with disease study. In vitro investigation is perhaps one of the most useful tools in ascertaining pathogen-host interaction. In vitro studies must, however, be complemented by observations on the natural course of infection in the species of interest to provide meaningful results. Data collection that assists field researchers in determining the health profile of a species or community should be incorporated in the research methodology. Much of this information can be gathered through direct field observation of behavior and mortality. Where possible, blood and other body fluid samples of all animals that are immobilized for any reason should be obtained. Collection and detailed evaluation of tissues from mortalities are also critical.

By learning the pathobiology of infectious agents, new areas of conservation application can be gained. The story of bovine brucellosis in bison (*Bison bison*) in Yellowstone National Park represents one example of the need for disease ecological research in wildlife management. Over one thousand bison have been culled in northern Yellowstone Park in order to prevent transmission of brucellosis from bison to livestock. In North America, brucellosis is a disease that causes infertility and abortion in cattle, elk (*Cervus elaphus*), and bison. Cattle and elk more often show these clinical signs; the disease does not usually affect bison. Initially introduced into bison from cattle, brucellosis has been virtually eradicated in Montana's livestock, leaving bison in Yellowstone as a potential reservoir of the disease. Around 50 percent of Yellowstone's

bison herd may be infected. Management practices to date have focused on adhering to government protocols on brucellosis-free certification within livestock. This provides a substantial economic benefit to livestock growers.

Nevertheless, there is still a relative lack of knowledge about the transmissibility of the bacterial infectious agent *Brucella abortus* between domestic cattle and wildlife in free-ranging situations (Zaugg et al. 1993; Williams et al. 1993; Meagher and Meyer 1994; Dobson and Meagher 1996; Roffe et al. 1999). The conservation implications are profound because the bison story encapsulates many of the issues conservation biologists must grapple with today: introduced alien species (in this case a pathogen); growing conflicts between humans, their domesticated animals, and wildlife; and increased population impacts of disease through cross-species transmission (brucellosis may be shared between resident Yellowstone bison and elk populations). With elk winter feeding stations concentrating animals, the management of one species obviously impacts another. *Brucella* is also a zoonotic organism capable of causing infection in people—although rare. More so, the brucellosis story is a shining example of the increasingly complex public policy arena facing conservation managers as they grapple with disease and health issues.

Putting Pathogens to Conservation Work: Potential Biomarkers

Beyond the health ramifications of disease, pathogens can also serve as potential tools for studying the ecology of populations and individuals. Understanding of disease-causing organisms and the pathogenesis of disease has markedly increased due to the availability of molecular tools. For instance, information gained from studies of the Retroviridae, the family of RNA viruses that include the human immunodeficiency virus (HIV), feline leukemia virus (FeLV), feline immunodeficiency virus (FIV), simian immunodeficiency virus (SIV), and others show how the specific biology of a pathogen can provide a specific signature of infection and evolution (Levy 1993; Leitner et al. 1996; Gao et al. 1999; Poss and Overbaugh 1999; Hahn et al. 2000).

Of specific interest are efforts relating viral genetic diversity with population structure of the host. Many of the retroviruses, like other viruses, have potential evolutionary rates approximately one million times higher than those of their vertebrate hosts (Ricchetti and Buc 1990). This suggests that viruses circulating in one population will be genetically distinct from those circulating in a different population (which has been well documented with HIV in humans) (Bachmann et al. 1994; Louwagie et al 1995). Furthermore, adjacent populations that exchange infected individuals can be distinguished from those that do not by examining the genetics of the resident viruses. In the former case the virus population will be randomly distributed, while in

the latter phylogenetic reconstruction of virus sequences will indicate distinct viral subpopulations (Poss and Overbaugh 1999). There is great potential benefit to applying these principles to wildlife species, as very recent changes in population dynamics are likely to be discernible due to rapid evolution of the viral genome.

By measuring viral genetic changes, we have the potential to use information that is used to determine contact and transmission of diseases between individuals and populations to delineate metapopulation dynamics of certain species such as mountain lions and lynx. This information can assist conservation managers in the determination of wildlife corridors and linkage areas and zones of wildlife and domestic animal contact.

Research Priorities in Conservation Medicine: Looking 10 Years Ahead

Disease affects every issue of concern to conservation biologists, including biodiversity, small or isolated population persistence, alien species introduction, and trophic cascades. Virtually any ecological perturbation that affects wildlife species can also alter the balance and composition of their pathogen communities. Future efforts in conservation need to incorporate the influence of disease on wildlife and of wildlife on disease. In this chapter, we provide key elements of a framework for inquiry that may assist conservation biologists in moving forward.

There are four broad areas for enhancement of the links between conservation biology and diseases of wildlife and humans:

1. *Expansion of interdisciplinary interaction.* Engage the talents of new disciplines to address conservation concerns. This can include the integration of conservation biology within existing disciplines such as veterinary and human medicine and social sciences such as economics (Rapport 1995). Medical and veterinary practitioners and researchers will certainly enrich their discipline by increasing their knowledge of how conservation issues such as biodiversity loss, climate and land-use change, and pollution influence human and animal health. Ecology and conservation biology become enriched when pathogens can be detected and their effects monitored.
2. *Integrated health and ecological assessment and monitoring.* Develop and refine environmental and physiological health assessment and monitoring protocols. The first step in conducting a current health assessment of an ecological system is to characterize the baseline health parameters for selected species or group of species (e.g., health indicator or sentinel species) and determine their responses to naturally fluctuating environmental variables. This includes monitoring variables that contribute to the physiological responses to stress within a population or in an individual (Hofer and East 1998). It will be neces-

sary to establish normal values for bioindicator species based on (1) existing archived data; (2) data from processing of stored, unanalyzed samples where appropriate; (3) opportunistic collections of material from both pristine and disrupted ecosystems; (4) targeted collections of appropriate materials from healthy specimens reflecting that specific ecosystem; and (5) new monitoring efforts. The development of testing protocols, identification of suitable diagnostic procedures and tests, identification of laboratory support, development of a quality-control-assurance plan for laboratory results, and development of data management and data analysis plans are all required to conduct a thorough assessment.

Sentinel species may assist in increasing monitoring efficiency at the ecosystem level. They can be utilized during rapid risk assessments to provide information on the environmental conditions of an area. Sentinel species or health indicator species can be selected for their ability to reflect environmental perturbations (Caro and O'Doherty 1999). Based on their life history and physiological attributes, selected species can provide insightful information about environmental changes at various spatial, temporal, and trophic scales. Given the complexity of ecosystems, sentinel species should be thought of as being specific to particular environmental conditions. In some cases, an assemblage of species may be suitable for providing an umbrella effect in monitoring the cumulative impacts of multiple environmental variables.

Beyond species- and population-oriented monitoring, ecological health information needs to be collected through ecosystem monitoring efforts, including long-term ecological monitoring. New research developments in determining ecological integrity should incorporate health assessment indicators (Karr and Chu 1995, 1999).

3. *Expanded diagnostic capability.* Present diagnostic efforts are focused on clinical testing of human or domestic animals. The potential for applying existing diagnostic capacity to health monitoring of wildlife species or those of conservation concern is relatively untapped. The limitation of financial resources has been a major barrier. Laboratory support for performing diagnostic testing in species other than humans and domesticated animals is minimal. Cross-species diagnostic testing, in which one laboratory can do comparative assessment of disease between species, is extremely rare and is usually found within a couple of national disease testing centers (e.g., USDA Research Labs, Centers for Disease Control, National Wildlife Health Center, and the Southeastern Cooperative Wildlife Disease Study).

Diagnostic laboratory testing can play an important role in monitoring the health of wildlife populations. During health evaluations, testing is necessary to detect exposure to an agent (serology), to identify the agents that are endemic in a population (bacteriology or virology) or to determine the cause of a catastrophic event such as a die-off or disease outbreak (clinical pathology, gross

BOX 8.1. Potential Research Priorities That Link Disease, Ecology, and Conservation Biology

1. Investigate vector-borne zoonotic diseases (such as mosquito-borne West Nile virus and malaria, sand fly-borne leishmaniasis, tick-borne Lyme disease, and bug-borne Chagas' disease).
 - What biotic and abiotic factors regulate vector populations? *Rationale for investigation:* Predators, parasites, and competitors may influence the population density and growth rates of arthropod vectors. Similarly, vectors are often limited by extremes in temperature and humidity, and those limitations may vary with life stage of the vector.
 - How do changes in climate influence vector populations, through either biotic or abiotic pathways? *Rationale for investigation:* Global climate change may influence both abundance and large- and small-scale distribution of vectors.
 - How do changes in land use influence vector populations, through either biotic or abiotic pathways? *Rationale for investigation:* Habitat destruction, conversion, and fragmentation may influence vectors directly or via their hosts or natural enemies, thereby affecting population size and variability.
 - What abiotic and biotic factors influence the proportion of vectors that are infected by the pathogen? *Rationale for investigation:* A key risk factor for many vector-borne diseases is the infection prevalence in the vector population. This can be influenced by abiotic factors that affect pathogen development and by ecological factors that affect the relative abundance of host species, which often vary in their competence as reservoirs for pathogens.
 - How does biodiversity affect disease risk? *Rationale for investigation:* High genetic or species diversity in the (reservoir) host community has recently been shown to reduce disease incidence in both human and crop systems.
2. Investigate directly transmitted zoonotic diseases (such as hantavirus pulmonary syndrome, Lassa fever and other arenaviral diseases, *Bartonella*).
 - What factors regulate reservoir populations? *Rationale for investigation:* For many directly transmitted zoonoses, rodents are the primary reservoirs. Rodent populations may be regulated by resource levels, predators, competitors, or pathogens (although most zoonotic pathogens appear relatively benign in reservoir hosts).
 - How do reservoir populations respond to changing climate, land use, and biodiversity? *Rationale for investigation:* Climate, land use, and diversity may influence reservoirs either directly, by allowing expansion or contraction of

geographic ranges or population sizes, or indirectly, by influencing biota that regulate reservoir populations.

- How does biodiversity in vertebrate communities affect disease risk? *Rationale for investigation:* High genetic or species diversity within vertebrate communities may regulate populations of reservoir species or otherwise reduce the probability of pathogen transmission.
 - How do local and global patterns of transportation influence the distribution of pathogens? *Rationale for investigation:* Travel by people and movements of ships and planes worldwide may introduce pathogens and their reservoirs or vectors to new areas.
3. Investigate water-borne and food-borne zoonotic diseases (such as *Vibrio cholera*, marine biotoxins and cyanobacteria, *Salmonella*, *Campylobacter*).
- How do changes in global temperature influence populations of pathogens, either free-living or commensal with other aquatic organisms? *Rationale for investigation:* Population growth of many water-borne pathogens is sensitive to water temperature, as is population growth of planktonic organisms with which pathogens may associate (e.g., *Vibrio cholerae*).
 - How do influxes of nutrients to lakes and estuaries influence populations of pathogens, either free-living or commensal with other aquatic organisms? *Rationale for investigation:* Population growth of many water-borne pathogens is sensitive to nutrient concentrations (e.g., nitrogen, phosphorus), as is population growth of planktonic organisms with which pathogens may associate. Human activities, such as livestock production, agriculture, and septic leakage, are often responsible for production and release of these nutrients.
4. Investigate noninfectious diseases (such as chronic and acute toxic effects of environmental contaminants; asthma; malignant tumors).
- To what degree are wildlife populations, especially those of conservation concern, affected by pollutants that decrease viability or reproductive success? *Rationale for investigation:* Evidence is mounting that sublethal effects of pollutants (e.g., endocrine mimics) can reduce population viability.
 - How do noninfectious diseases interact in wildlife populations? *Rationale for investigation:* Noninfectious agents may reduce effectiveness of the immune system, thereby influencing the ability of organisms to resist other environmental insults.

Sources: Ostfield and Keesing 2000a; Zhu et al 2000.

pathology, histopathology). Tests can be used for epizootic and epidemiologic purposes and can estimate prevalence, incidence, and geographic distribution of selected disease agents; determine infection in subpopulations; and delineate intra- and interspecific disease transmission. The results of diagnostic testing are most useful in complementing thorough field-based ecological research. Ecological studies provide the necessary context for any results concerning disease dynamics and can even discern certain physiological responses due to stress imposed on populations by environmental change (Hofer and East 1998).

4. *Resolution of human and wildlife conflict—implementing conservation medicine practice in conservation reserve design and management.* With increasing fragmentation of habitat, the consequences of enhanced human and animal conflicts are more apparent. Disease is only one manifestation of this global phenomenon. Nevertheless, conservation managers need to be savvy in developing management scenarios that minimize disease impacts. Buffer zones and wildlife corridors may require new designs to mitigate or diminish disease threats. Resolving human and wildlife conflicts is the challenge ahead in conservation. Those conflicts include the interaction between domesticated animals and wildlife. With growing intrusions of people and their animals into wildland areas, such as livestock grazing on public lands, salmon aquaculture pens in coastal marine areas, primate ecotourism in the tropics, and the influx of backpackers with their dogs into designated wilderness areas, disease mitigation will be a major factor in conservation management. The design and management of conservation reserves need to be open to the consequences of disease threats—not as a marginal issue of concern, which is the case at this time, but as an issue more central to achieving long-term conservation success.

Conclusions

For many of the research questions presented in this chapter, answers will come from a combination of monitoring, modeling, experimentation, and comparison. Monitoring is crucial for detecting changes in disease distribution or incidence as a result of human-caused changes in climate, land use, or pollutant concentration. For example, surveillance for diseases using sentinel animals can provide advance warning of changes in distribution or virulence of pathogens, and suggest possible causes. Modeling allows exceedingly complex parts of nature to be abstracted; relationships among populations, species, habitats, and ecosystems to be specified; the logic of interactions to be clarified; and specific hypotheses to be derived. Experimentation is important for testing specific hypotheses on relatively small scales, and for determining mechanisms for observed patterns at larger scales or within more complex, inclusive systems. For instance, effects of biodiversity or habitat destruction

on the maintenance and transmission of pathogens can be examined in a laboratory setting by experimentally altering diversity or landscape patterns and measuring responses.

Comparative methods are analogous to experiments but consist of monitoring effects of conditions that have not been experimentally manipulated and differ between systems in specific ways. For example, population dynamics of an imperiled species can be monitored before and after a toxic spill, or inside and outside an area where a pathogen has invaded. Effects of diminishing biodiversity on vector-borne vs. directly transmitted diseases may elucidate the influence of transmission mode on ecology of infectious diseases.

Ecological studies of infectious and noninfectious diseases are therefore crucial to understanding, predicting, and reducing risk to the health of humans, domesticated animals, and wildlife and the environment that sustains them. Conservation medicine can provide new skill sets to address disease impacts in conservation. These include the incorporation of biomedical research and resources in conservation problem solving; the development of diagnostic methods that examine ecological and health parameters; and the design and implementation of integrated health and ecological assessment models.

LITERATURE CITED

- Aguirre, A. A., D. E. Hansen, E. E. Starkey, and R. G. McLean. 1995. Serologic survey of wild cervids for potential disease agents in selected national parks in the United States. *Preventive Veterinary Medicine* 21:313–322.
- Aguirre, A. A., R. G. McLean, R. S. Cook, and T. J. Quan. 1992. Serologic survey for selected arboviruses and other potential pathogens in wildlife from Mexico. *Journal of Wildlife Diseases* 28:435–442.
- Aguirre, A. A., and E. E. Starkey. 1994. Wildlife disease in U.S. national parks: Historical and coevolutionary perspectives. *Conservation Biology* 8:654–661.
- Aguirre, A. A., E. E. Starkey, and D. E. Hansen. 1995. Wildlife diseases in national park ecosystems. *Wildlife Society Bulletin* 23:415–419.
- Anderson, E. C. 1995. Morbillivirus infections in wildlife (in relation to their population biology and disease control in domestic animals). *Veterinary Microbiology* 44(2–4): 319–332.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light gaps, and pathogens. *Ecology* 65:1705–1712.
- Bachmann, M. H., E. L. Delwart, E. G. Shpaer, P. Lingenfelter, R. Singal, J. I. Mullins. 1994. Rapid genetic characterization of HIV type 1 strains from four World Health Organization–sponsored vaccine evaluation sites using a heteroduplex mobility assay. *AIDS Research and Human Retroviruses* 10(11):1345–1353.
- Blais, J. M., D. W. Schindler, D. C. G. Muir, D. B. Donald, and B. Rosenberg. 1998. Accumulation of persistent organochlorine compounds in mountains of western Canada. *Nature* 395: 585–588.

- Blaustein, A. R., P. D. Hoffman, D. G. Hokit, and J. M. Kiesecker. 1994. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines. *Proceedings of the National Academy of Sciences* 91:1791–1795.
- Blaustein, A. W., and D. B. Wake. 1995. The puzzle of declining amphibian populations. *Scientific American* (April): 52–57.
- Caro, T. M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. *Conservation Biology* 13(4):805–814.
- Colborn, T., D. Dumanoski, and J. P. Meyers. 1996. *Our Stolen Future*. New York: Dutton.
- Colborn, T., R. S. vom Saal, and A. M. Soto. 1993. Developmental effects of endocrine-disrupting chemicals in wildlife and humans. *Environmental Health Perspectives* 101:378–384.
- Dobson, A. P., and R. M. May. 1986. Disease and conservation. In M. Soulé (ed.), *Conservation Biology: The Science of Scarcity and Diversity*, pp. 345–365. Sunderland, Mass.: Sinauer Associates.
- Dobson, A. P., and M. Meagher. 1996. The population dynamics of brucellosis in the Yellowstone National Park. *Ecology* 74(4):1026–1036.
- Dye, C. 1996. Serengeti wild dogs: What really happened? *Trends in Ecology and Evolution* 11:188–189.
- Epstein, P. R. 1995. Emerging diseases and ecosystem instabilities: New threats to public health. *American Journal of Public Health* 85:168–172.
- Epstein, P. R. 1997. Climate, ecology, and human health. *Consequences* 3(2):2–19.
- Epstein, P. R. 1999. Climate and health. *Science* 285:347–348.
- Epstein, P. R., A. Dobson, and J. Vandermeer. 1997. Biodiversity and emerging infectious diseases: Integrating health and ecosystem monitoring. F. Grifo and J. Rosenthal (eds.), *Biodiversity and Human Health*. Washington, D.C.: Island Press.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Frankel, O. H., and M. E. Soulé. 1981. *Conservation and Evolution*. Cambridge, U.K.: Cambridge University Press.
- Gao, F., E. Bailes, D. L. Robertson, Y. Chen, C. M. Rodenburg, S. F. Michael, L. B. Cummins, L. O. Arthur, M. Peeters, G. M. Shaw, P. M. Sharp, and B. H. Hahn. 1999. Origin of HIV-1 in the chimpanzee *Pan troglodytes troglodytes*. *Nature* 397(6718):436–441.
- Gilbert, G. S. 1995. Rain forest plant diseases: The canopy-understory connection. *Selbyana* 16:75–77.
- Ginsberg, J. R., et al. 1995. Handling and survivorship of African wild dog (*Lycaon pictus*) in five ecosystems. *Conservation Biology* 9:665–674.
- Grenfell, B. T., and Dobson, A. P. 1995. *Population Dynamics of Infectious Diseases in Natural Populations*, Cambridge, U.K.: Cambridge University Press.
- Hahn, B. H., G. M. Shaw, K. M. De Cock, and P. M. Sharp. 2000. AIDS as a zoonosis: Scientific and public health implications. *Science* 287(5453):607–614.
- Heinsohn, R. 1992. When conservation goes to the dogs. *Trends in Ecology and Evolution* 7:214–215.

- Hofer, H., and M. L. East. 1998. Biological conservation and stress. *Advances in the Study of Behavior* 27:405–525.
- Hollings, C. S., D. W. Schindler, B. W. Walker, and J. Roughgarden. 1995. Biodiversity in the functioning of ecosystems: An ecological synthesis. In C. Perrings, K.-G. Maler, C. Folke, C. S. Hollings, and B.-O. Jansson (eds.), *Biodiversity Loss: Economic and Ecological Issues*, pp. 44–83. New York: Cambridge University Press.
- Hubalek, Z., and J. Halouzka. 1999. West Nile fever—A reemerging mosquito-borne viral disease in Europe. *Emerging Infectious Diseases* 5:643–650.
- Karr, J. R., and E. W. Chu. 1995. Ecological integrity: Reclaiming lost connections. In L. Westra and J. Lemons (eds.), *Perspectives on Ecological Integrity*, pp. 34–48. Dordrecht, Netherlands: Kluwer.
- Karr, J. R., and E. W. Chu. 1999. *Restoring Life in Running Waters: Better Biological Monitoring*. Washington, D.C.: Island Press.
- Lanciotti, R. S., J. T. Roehrig, V. Deubel, et al. 1999. Origin of the West Nile virus responsible for an outbreak of encephalitis in the northeastern United States. *Science* 286:2333–2337.
- Laurance, W. F., K. R. McDonald, and R. Speare. 1996. Epidemic disease and the catastrophic decline of Australian rain forest frogs. *Conservation Biology* 10(2): 406–413.
- Leitner, T., D. Escanilla, C. Franzen, M. Uhlen, and J. Albert. 1996. Accurate reconstruction of a known HIV-1 transmission history by phylogenetic tree analysis. *Proceedings of the National Academy of Sciences USA* 93(20): 10864–10869.
- Levy, J. A. 1993. Pathogenesis of human immunodeficiency virus infection. *Microbiological Reviews* 57(1): 183–289.
- Louwagie, J., W. Janssens, J. Mascola, L. Heyndrickx, P. Hegerich, G. van der Groen, F. E. McCutchan, and D. S. Burke. 1995. Genetic diversity of the envelope glycoprotein from human immunodeficiency virus type 1 isolates of African origin. *Journal of Virology* 69(1): 263–271.
- McMichael, A. J. 1997. Global environmental change and human health: Impact assessment, population vulnerability, and research priorities. *Ecosystem Health* 3:200–210.
- McMichael, A. J., B. Bolin, R. Costanza, G. C. Daily, C. Folke, K. Lindahl-Kiessling, B. Lindgren, and E. Niklasson. 1999. Globalization and the sustainability of human health: An ecological perspective. *Bioscience* 49(3):205–210.
- McMichael, A. J., and A. Haines. 1997. Global climate change: The potential effects on health. *British Medical Journal* 315:805–809.
- Meagher, M., and M. E. Meyer. 1994. On the origin of brucellosis in bison in Yellowstone National Park: A review. *Conservation Biology* 8:645–653.
- Meffe, G. 1999. Conservation medicine. *Conservation Biology* 13: 953–954.
- Ostfeld, R. S., and F. Keesing. 2000a. Biodiversity and disease risk: The case of Lyme disease. *Conservation Biology* 14:722–728.
- Ostfeld, R. S., and F. Keesing. 2000b. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *TREE* 14(12): 483–488.

- Patz, J. A., P. R. Epstein, T. A. Burke, and J. M. Balbus. 1996. Global climate change and emerging infectious diseases. *JAMA* 275:217–223.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321–326.
- Pokras, M., G. M. Tabor, M. Pearl, D. Sherman, and P. Epstein. 1999. Conservation medicine: An emerging field. In P. K. Raven (ed.), *Nature and Human Society: The Quest for a Sustainable World*, pp. 551–556. Washington, D.C.: National Academy Press.
- Poss, M., and J. Overbaugh. 1999. Variants from the diverse virus population identified at seroconversion of a clade A human immunodeficiency virus type 1-infected woman have distinct biological properties. *Journal of Virology* 73(7): 5255–5264.
- Rappole, J. H., S. R. Derrickson, and Z. Hubalek. 2000. Migratory birds and spread of West Nile virus in the Western Hemisphere. *Emerging Infectious Diseases* 6:319–328.
- Rapport, D. J. 1995. Ecosystem health: An emerging transdisciplinary science. In D. J. Rapport, C. Gaudet, and P. Calow (eds.), *Evaluating and Monitoring the Health of Large-Scale Ecosystems*, pp. 5–31. Heidelberg: Springer-Verlag.
- Rees, W. E. 1996. Revisiting carrying capacity: Area-based indicators of sustainability. *Population and Environment* 7:195–215.
- Reisen, W. K., R. P. Meyer, M. M. Milby, et al. 1992. Ecological observations on the 1989 outbreak of St. Louis encephalitis virus in the southern San Joaquin Valley of California. *Journal of Medical Entomology* 29:472–482.
- Ricchetti, M., and H. Buc. 1990. Reverse transcriptases and genomic variability: The accuracy of DNA replication is enzyme specific and sequence dependent. *European Molecular Biology Organization Journal* 9(5): 1583–1593.
- Roelke-Parker, M. E., L. Munson, C. Packer, R. Kock, S. Cleaveland, M. Carpenter, S. J. O'Brien, A. Pospischil, R. Hofmann-Lehmann, H. Lutz, et al. 1996. A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature* 379(6564): 441–445.
- Roffe, T. J., J. C. Rhyan, K. Aune, L. M. Philo, D. R. Ewalt, T. Gidlewski, and S. G. Hennager. 1999. Brucellosis in Yellowstone National Park bison: Quantitative serology and infection. *Journal of Wildlife Management* 63(4):1132–1137.
- Rogers, D. J., and S. E. Randolph. 2000. The global spread of malaria in a future, warmer world. *Science* 289:1763–1766.
- Schindler, D. W. 1999. From acid rain to toxic snow. *Ambio* 28: 350–355.
- Schulze, E.-D., and H. A. Mooney (eds.). 1994. *Biodiversity and Ecosystem Function*. Berlin: Springer-Verlag.
- Thorne, E. T., and E. S. Williams. 1988. Disease and endangered species: The black-footed ferret as a recent example. *Conservation Biology* 2:66–74.
- Van der Putten, W. H., and C. D. Van der Stoep. 1998. Plant parasitic nematodes and spatio-temporal variation in natural vegetation. *Applied Soil Ecology* 10:253–262.
- Van der Putten, W. H., et al. 1993. Plant-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362:53–56.
- van Riper III, C., et al. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* 56:327–344.

- Walsh, J. F., D. H. Molyneux, M. H. Birley. 1993. Deforestation: Effects on vector-borne disease. *Parasitology* 106:S55–S75.
- Warner, R. E. 1968. The role of introduced diseases in the extinction of the endemic Hawaiian avifauna. *Condor* 70:101–120.
- Williams, E. S., et al. 1988. Canine distemper in black-footed ferrets (*Mustela nigripes*) from Wyoming. *Journal of Wildlife Diseases* 24:385–398.
- Williams, E. S., E. T. Thorne, S. L. Anderson, and J. D. Herriges Jr. 1993. Brucellosis in free-ranging bison (*Bison bison*) from Teton County, Wyoming. *Journal of Wildlife Diseases* 29(1):118–122.
- Wilson, E. O. 1988. The current state of biological diversity. In E. O. Wilson (ed.), *Biodiversity*, pp. 3–19. Washington, D.C.: National Academy Press.
- Wilson, E. O. 1992. *The Diversity of Life*. Cambridge, Mass.: Belknap Press.
- Woodwell, G. M., and R. A. Houghton. 1990. The experimental impoverishment of natural communities effects of ionizing radiation on plant communities: 1961–1976. In G. M. Woodwell (ed.), *The Earth in Transition: Patterns and Processes of Biotic Impoverishment*, pp. 9–24. Conference, Woods Hole, Massachusetts, USA, October 1986. Cambridge, U.K.: Cambridge University Press.
- Zaugg, J. L., S. K. Taylor, B. C. Anderson, D. L. Hunter, J. Ryder, and M. Divine. 1993. Hematologic, serologic values, histopathologic and fecal evaluations of bison from Yellowstone Park. *Journal of Wildlife Diseases* 29(3):453–457.
- Zhu, Y. Y., et al. 2000. Genetic diversity and disease control in rice. *Nature* 406:718–722.

GLOBAL ENVIRONMENTAL CHANGE

Effects on Biodiversity

William H. Schlesinger, James S. Clark,
Jacqueline E. Mohan, and Chantal D. Reid

On December 19, 1999, the *New York Times* proclaimed, "1999 Continues Warming Trend Around Globe," thus confirming the reminiscence of many U.S. citizens of colder winters just a few decades ago. Supplementing the historical records from weather stations, surrogate measures of climate change confirm a rise in global temperature—showing a reduction in the extent and thickness of arctic sea ice (Johannessen et al. 1999; Rothrock et al. 1999), shorter ice-covered seasons on many northern lakes (Robertson et al. 1992), earlier arrival and activity of springtime plants and animals (Ahas 1999), and rising satellite-measured temperatures of Earth's upper atmosphere (Wentz and Schabel 2000). Changes in the distribution and abundance of Earth's biota also tell us that a warming trend is in progress. During the past few decades, the distributions of birds, butterflies, and trees have all shifted northward, consistent with a warming of Earth's climate. Scientists of the Intergovernmental Panel on Climate Change (IPCC) weigh the evidence that this change in climate is due to anthropogenic changes in the chemistry of our environment, namely the continuing rise of carbon dioxide (CO₂) and other trace gases in Earth's atmosphere (Santer et al. 1996; Tett et al. 1999).

As with past changes in climate, the current global warming may change the distribution of Earth's species, leading to entirely new assemblages of species in ecological communities. When climate change is slow, species can adapt or migrate to new habitats, changing their distribution or range to adjust to the new conditions. However, future changes in global climate, wrought by humans, may be so rapid as to overwhelm the natural ability of plants and animals to disperse to new habitats (Overpeck et al. 1991; Davis and Zabinski 1992). If species cannot change their distribution fast enough, will they go extinct?

In this chapter, we define global change more broadly than climate change alone. We focus on a variety of environmental changes that are global in extent (e.g., climate and rising CO₂) or global inasmuch as they affect large regions on several continents (e.g., rising concentrations of tropospheric ozone and nitrogen availability). Our objectives are (1) to review past changes in global climate for evidence of their effects on biodiversity, especially during the transition from glacial to interglacial periods; (2) to analyze what recent field experiments tell us about the effects of anticipated future environmental changes on biodiversity; and (3) to suggest research priorities in conservation biology that can help remove uncertainties about biotic responses to global change. We ask: Is the ongoing human-induced global environmental change a threat to biodiversity?

Community Structure:

Changes in Biodiversity with Stress and Subsidy

In a seminal paper entitled "Perturbation Theory and the Subsidy-Stress Gradient," Odum et al. (1979) noted that many of the changes seen when ecological communities are provided with supplemental resources (e.g., fertilizer) resemble changes seen when communities are exposed to toxic substances. Applications of fertilizer for more than one hundred years on the Parkgrass experimental plots at Rothamstead (figure 9.1) reduced the length of the dominance-diversity curves (i.e., lowering richness) and increased their slope (i.e., decreasing equitability). (A dominance-diversity curve is a plot of the abundance of each species in a community of plants or animals as a function of its rank in abundance, from the most important species to the least.) Similar changes in dominance-diversity curves occur when communities are exposed to toxic effluents, such as from smelters (e.g., figure 9.2). In both cases, the changes in the dominance-diversity curves are the reverse of what is seen during the progressive recovery of communities following disturbance (e.g., Bazzaz 1975), leading Whittaker (1972) to call these trends "retrogressive."

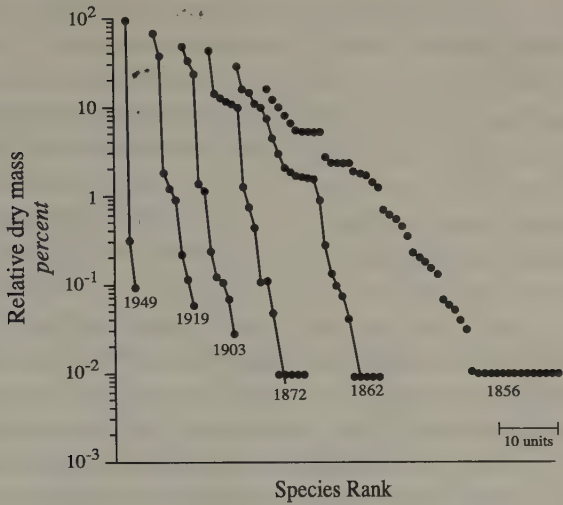


FIGURE 9.1. Plant species diversity in pasture in the Parkgrass experiment at Rothamstead, United Kingdom, following the continuous application of nitrogen fertilizer from 1856 to 1949. At each sampling, fewer species were present, and there was an increasing concentration of dominance in the most abundant species. From Kempton (1979).

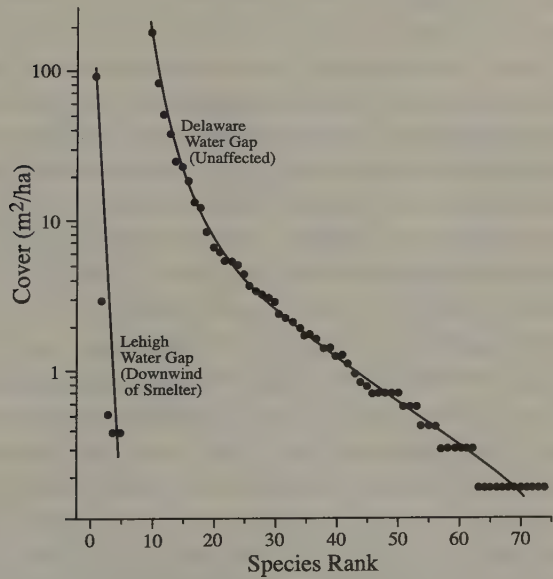


FIGURE 9.2. Cover of lichen species as a function of the decreasing rank of species in ground samples taken in Delaware Water Gap (unpolluted) and Lehigh Water Gap (polluted) environments in southern Pennsylvania. From Nash (1975).

At first glance, many of the global changes wrought by humans might appear to be beneficial in the context of Odum's stress-subsidy theory. Rising CO₂, warmer temperatures, greater precipitation, and increased nitrogen availability should stimulate the rate of plant growth in many regions. Moreover, rising plant production and a more clement climate might benefit many animal populations. However, nearly three decades ago, Rosenzweig (1971) postulated that enrichment would destabilize model ecosystems, lowering their diversity. Although subsequent experimental work has not always confirmed the theory (e.g., McCauley and Murdoch 1990), Rapport et al. (1985) found that a loss of species diversity was the most consistent indicator of ecosystem retrogression, caused by either stress or subsidy. Many ecosystem-level experiments simulating global change phenomena show losses of diversity that should warn us of the vulnerability of biodiversity to global environmental change. Prehistoric evidence of the retrogressive impacts of environmental change can be found in the species composition and dominance-diversity relationships of seafloor communities now preserved in the fossil record of mid-Cretaceous black shales (Sageman and Bina 1997). As human perturbation of the environment becomes global in extent, lower biotic diversity will result not only from the local disappearance of species, but also from global extinction.

The Last Great Global Warming: The End of the Pleistocene

The end of the last ice age, 10,000 years ago, provides an opportunity to examine how biodiversity responded to climate change at continental scales. However, in many ways, the transition to warmer postglacial conditions is not a perfect analog to the future greenhouse warming of our planet. The latitudinal distribution of incoming radiation (Kutzbach and Guetter 1986), the presence of continental ice sheets (Clark et al. 1999), an unusual pattern of ocean circulation (Broecker 1997), lower sea level (Fairbanks 1989), and a unique distribution of vegetation (Foley et al. 1994) produced a different distribution of climate change than what we expect from future greenhouse warming. Atmospheric CO₂ rose from ~200 ppm (parts per million by volume) to ~280 ppm between 15,000 and 9,000 years ago (Barnola et al. 1987), but that increase may not have had the same effects on biodiversity as the current trend, which will soon reach 600 ppm and above (Collatz et al. 1998). Because climate change depends on factors that control atmospheric circulation, we can expect the future greenhouse warming to differ from past global change in its rate and the seasonality of temperature and precipitation.

Despite the fact that the anticipated greenhouse warming differs from past climate changes, the end of the Pleistocene provides valuable perspective. Because it is recent, the fossil record is more complete for the last glacial period than it is for prior glacial cycles. The fossil record, ice-core evidence,

and climate models agree that global mean temperature increased 4–7°C at the end of the Pleistocene (Kutzbach and Guetter 1986; Kutzbach et al. 1993; Wright et al. 1993). A temperature change of about the same magnitude is expected during the next century. Although the anticipated global warming will occur, on average, more rapidly than that of recent glacial cycles, some of the warming during deglaciation also happened quickly. For instance, a period of warming ~11,650 years ago occurred over a course of a few decades (Taylor et al. 1997), possibly similar to the rate of climate change anticipated during this century.

Extinctions

There is clear evidence for mass extinctions of large mammals at the end of the Pleistocene but limited evidence for the extinction of plant species. Paleontologists debate whether the animal extinctions resulted from changes in vegetation set in motion by climate change or from human hunting. Several overview volumes discuss this issue in detail (Martin and Klein 1984; MacPhee 1999).

The limited evidence for plant extinctions at the end of the Pleistocene may reflect, in part, limitations of the fossil record. An extensive record of fossil pollen provides evidence for distributions of many taxa (COHMAP 1988), but generally similar species cannot be distinguished, and the record is biased toward wind-dispersed species and those that occur in regions where lakes and mires preserve a sedimentary record. Packrat middens provide fossil records of plant occurrence in arid regions, but these records are often discontinuous in space and time. Thus, more extinctions may have occurred than are apparent from the fossil evidence. At least one extinction, that of the once extensive spruce *Picea critchfieldii*, has been documented from deposits of cones and needles in the southeastern United States (Jackson and Weng 1999). This species was apparently abundant across the region before ten thousand years ago and may have died out as temperatures began to rise. Unlike the case of faunal extinctions, humans probably played no direct role in its demise. Dispersal limitation is an obvious candidate for this species' failure to survive into the Holocene, suggesting that even widely distributed and abundant species can be at risk. The loss of this once extensive species has obvious implications for the losses of biodiversity that may accompany future global warming.

Evolutionary Change

Although the fossil record provides few examples of plant extinctions, molecular studies indicate losses of intraspecific genetic diversity since the Pleistocene. In many cases, the losses appear to be related to founder effects—the limited genetic diversity that arises when a new population is derived from

only a few individuals (Ibrahim et al. 1996). Molecular data show that genetic diversity for many plant populations declines with increasing distance from refugia—areas where the populations survived during times of glacial expansion (Comes and Kadereit 1998). Migrational barriers appear to have slowed the northward spread of some genotypes and led to dominance by a subset of the haplotypes (groups of plants that are all descended from the same maternal ancestor) that may have been widely separated in different Pleistocene refugia. Modern haplotype distributions suggest that the east-west trending mountain ranges of western Europe, especially the Alps, were barriers for the spread of many genotypes (Hewitt 1999, 2000). A pattern of decreasing genetic diversity with distance from past refugia is consistent with the theoretical loss of genetic diversity that would be expected during long-distance founding events (LeCorre et al. 1997).

Not all evolutionary responses to past warming involved net losses of diversity. The mixing of previously segregated genotypes during migrations can also influence genetic diversity. For example, a large molecular data set from white oaks across Europe, which includes eight species and twenty-three haplotypes, suggests that migration pathways from southern European refugia crossed one another, thus producing mixtures of haplotypes (Dumolin-Lapeque et al. 1997). This pattern is especially evident in western Europe, where closely related species may have occupied as many as four different refugia, subsequently expanding into overlapping ranges in central and northern Europe. Taken together, the accumulating molecular evidence suggests that the broad-scale migrations that attend climate change are epochs of evolutionary change that may include both losses of diversity and additions of new genotypes.

Range Shifts

The fossil record shows that dramatic rearrangements of species have occurred during climate changes over areas of low relief, such as eastern North America (Davis 1981; Delcourt and Delcourt 1987) and western Europe (Huntley and Birks 1983). Ecologists have examined the Pleistocene record of these migrations to address the potential for biota to respond to current global warming (Pitelka et al. 1997; Clark 1998; Clark et al. 2001; Cain et al. 1998). "Isopoll maps," showing interpolated contours of equal pollen abundance in lake sediments, suggest rates of northward spread from 50 to 1,000 m per year for many trees since the end of the Pleistocene (Davis 1981; Huntley and Birks 1983; Ritchie and MacDonald 1986). Such rates were equaled or exceeded by some beetles (Coope 1987) and even flightless grasshoppers (Hewitt 1990). These rates are less than the rates of migration that would be needed to accommodate anticipated climate change—1,000 to

5,000 m per year during the next several centuries (Overpeck et al. 1991). The paleoestimates do not, however, rule out the potential for more rapid migration, because the distribution of past ecosystems may have been constrained by rates of climate change.

In many cases, ranges of populations both extended on their northern boundaries and retracted on their southern ones. However, migrations in response to global warming entail more than a northward shift in range limits; geography imposes barriers to dispersal and fragments opportunities for growth and survival. For example, the meadow grasshopper (*Chorthippus parallelus*) of Europe and Siberia appears to have occupied distinct glacial refugia in Spain, Italy, Greece, and Turkey. Today, the northern European populations of these grasshoppers are dominated by the Balkan genotype, perhaps because postglacial migration of populations in Spain and Italy was restricted by the Pyrenees and Alps (Hewitt 1999). Likewise, European beech (*Fagus sylvatica*) occurred in both Italy and the Carpathians, but the Alps appear to have blocked expansion of the Italian populations (Demesure et al. 1996); modern populations in northern Europe are derived only from Carpathian populations. Haplotype distributions for vertebrates suggest similar effects of dispersal barriers on postglacial spread (Hewitt 1999, 2000).

In many cases, species occupying similar regions today were allopatric (not occurring in the same region) during glacial periods, and many came to occupy their modern range by very different migrational pathways (Graham and Grimm 1990; Taberlet et al. 1998). Whereas European beech apparently failed to traverse the Alps from its Pleistocene refuge in Italy (Demesure et al. 1996), oaks expanded northward from Italian populations (Dumolin-Lapeque et al. 1997). In eastern North America, hemlock (*Tsuga*) and beech (*Fagus grandifolia*), which today are dominant species in northern hardwood forests, arrived at their modern distributions predominantly by way of the Appalachians and the Coastal Plain, respectively. The fact that the modern distribution of species appears to derive from different migration patterns in the past suggests that it may be difficult to ensure appropriate corridors for biotic migration in the future.

Rapid range expansions could have unexpected effects on biodiversity, especially if species escape from competitors, predators, pollinators, pathogens, and so forth. For example, during rapid postglacial warming, many insects reached Britain before most temperate tree species arrived. Coope (1987) suggests that the ground beetle (*Calosoma inquisitor*) must have preyed on caterpillar species that fed on birch trees that dominated British forests at the time, despite the fact that modern *Calosoma* prey almost exclusively on caterpillars that feed on oaks. The changes in assemblages indicated

by the fossil record (e.g., Davis 1981; Graham and Grimm 1990) imply reorganization of trophic relationships and novel food webs.

The potential for the survival of species during climate change is higher in varied topography, such as in the western United States and southern Europe, than in regions of low relief (Van Devender and Spaulding 1979). Elevational shifts in the distribution of species in montane regions occurred throughout the globe as a result of gradients in temperature, moisture, and perhaps even CO₂ (Street-Perrott et al. 1997). For example, the highly dissected topography in northern Queensland provided the necessary habitat for rain forest species to persist in the face of regional aridity during the Pleistocene (Hopkins et al. 1990). Mesic valleys on the eastern edge of the Atherton tableland appear to have harbored rain forest, and expansion onto the tableland occurred as moisture levels increased in the Holocene (Walker and Chen 1987; Kershaw 1993).

Range expansion across areas where suitable habitats are scarce generally requires long-distance dispersal. In the case of forest trees, both fossil pollen and molecular data suggest that rare long-distance dispersal events have been important. The fossil record demonstrates dispersal across obstacles such as the North Sea (Reid 1899); the Baltic (Kullman 1996), and the Great Lakes (Webb 1987; Woods and Davis 1989). The dominance of an area by a single haplotype is consistent with models of long-distance dispersal, in which early arrivals rapidly come to dominate a population.

Summary

The fact that rapid spread may have occurred in the past is no insurance of future potential. The molecular evidence for mountain barriers to dispersal, and the extinction of at least one dominant forest species in eastern North America (Jackson and Weng 1999), indicate that the vegetation of the past did not uniformly track climate change. Moreover, the processes that make long-distance dispersal possible (involving winds, waters, and biotic vectors) are different today than they were in the past. Human activities could slow population spread by fragmenting the available habitat and by introducing alien species that affect the survival and spread of native species. Humans accelerate the spread of species through introductions and transport (Vitousek et al. 1996; Clark, Beckage et al. 2001). Some species benefit from accidental and intentional introductions by humans, whereas present or potential ranges of other species shrink due to competition, predation, and disease associated with exotics. As yet, the paleorecord of the response of biodiversity to global change has not provided us with general predictions that can be applied to current global warming. Given the critical importance of extreme dispersal events in mediating overall rates of population spread, future research should focus on factors responsible for long-distance dispersal.

One valuable insight gained from studies of paleoecology is an appreciation of the breadth of response to past climate change. While many species occupy new ranges sufficiently fast to track climate change, others do not. Lessons from the end of the Pleistocene include cautions that even widely distributed species may not survive rapid climate change.

Anticipated Global Climate Change

In this section we discuss projected changes in temperature and moisture, and the expected repercussions of these changes.

Temperature

The ranges of many plants and animals are correlated with temperature, particularly extremes of cold temperature that can kill most individuals in exceptional years. For instance, the northern distribution of creosotebush (*Larrea tridentata*) in the arid Southwest is correlated with minimum temperatures lower than -16°C , which cause freezing and cavitation of its xylem elements (Pockman and Sperry 1997). The deciduous trees of eastern North America extend to the -40°C minimum temperature isotherm, beyond which conifers of the boreal forest spread northward (Arris and Eagleson 1989). The northern edge of the winter range of the eastern phoebe (*Sayornis phoebe*) is correlated with the -4°C average minimum January temperature (Root 1988). Such correlations suggest that the ranges of species will shift northward with warming temperatures, consistent with recent studies of the historical distribution and activity of birds (Thomas and Lennon 1999; Dunn and Winkler 1999), butterflies (Parmesan et al. 1999; Roy and Sparks 2000), and white spruce (*Picea mariana*; Payette and Filion 1985). Satellite measures of “greenness” indicate a general northward expansion in the activity of vegetation with global warming (Myneni et al. 1997).

Similarly, the elevational distribution of plants and animals will change with changes in climate (Jobbagy and Jackson 2000). In the western United States, the distribution of chipmunks and ground squirrels on mountains is determined by the thermal tolerance of each species (Heller and Gates 1971; Hudson and Deavers 1973). With global warming, each species would be expected to occur at higher elevations, and some species may disappear from the highest portions of low mountains, as happened during the global warming that ended the last glacial period (Brown 1971). Similarly, the occurrence of lake trout in northern lakes is determined by cold waters—a habitat that may disappear when shallow lakes experience warmer temperatures (Schindler et al. 1990).

Rising temperatures of coastal waters are also a putative cause of a decline in the abundance of marine zooplankton (Roemmich and McGowan 1995), the poor recruitment of North Sea cod (*Gadus morhua*); O'Brien et al. 2000),

and the widespread bleaching and loss of corals in many tropical seas (Glynn 1996; Brown 1997; Warner et al. 1999; Aronson et al. 2000). Predation by the sea star, *Pisaster*, in marine intertidal communities is lower during periods of warm ocean waters, reducing its role as a keystone predator (Sanford 1999). A resampling of marine intertidal communities at the Hopkins Marine Station (Monterey Bay) showed large changes in macroinvertebrate species during the past sixty years, apparently associated with warmer seawater temperatures (Sagarin et al. 1999). Most southern species increased in abundance, while northern species declined (Barry et al. 1995). At its extreme, global warming could lead to major changes in the circulation of ocean currents and flooding of coastal ecosystems and coral reefs by rising sea level.

Relatively few experiments have examined climatic warming at the ecosystem level. John Harte established one of the most realistic field studies at the Rocky Mountain Biological Laboratory in the mountains of central Colorado. Using overhead infrared heaters to apply 22 W/m^2 to the soil surface, Harte and Shaw (1995) were able to increase the total average downward radiation by 3 percent in replicate plots of alpine meadow, raising the surface temperature to values expected with a doubled- CO_2 atmosphere. Price and Waser (2000) report no changes in plant community composition over the first four years of the experiment, which they attribute to drier soils in the warmed plots. However, the field-warming experiment increased the length of the growing season, because spring snowmelt advanced by seven days in the warmed plots (Harte et al. 1995), where Price and Waser (1998) documented earlier flowering in several herbs. The importance of changes in the length of the growing season, rather than changes in temperature *during* the growing season, is also seen in studies that have manipulated the duration of the winter snowpack in alpine habitats (Bell and Bliss 1979; Galen and Stanton 1993, 1995).

Experimental manipulations of ecosystem temperature across a range of sites in arctic tundra show dramatic changes in the rate of plant development, also due to changes in the length of the growing season (Arft et al. 1999). Over a nine-year experiment in Alaska, elevated temperatures increased the growth of shrubs, at the expense of nonvascular plants, largely mosses (Chapin et al. 1995). Losses of species and steepening of dominance-diversity curves during the course of the experiment are indicative of biotic impoverishment (figure 9.3). Grime et al. (2000) report changes in plant community composition during a five-year soil warming experiment in British grasslands, with the largest changes seen in an early-successional field.

Whole-ecosystem manipulations of temperature are more difficult to establish in forest vegetation, but several researchers have attempted soil warming experiments (Peterjohn et al. 1993). On Cape Cod, a soil warming

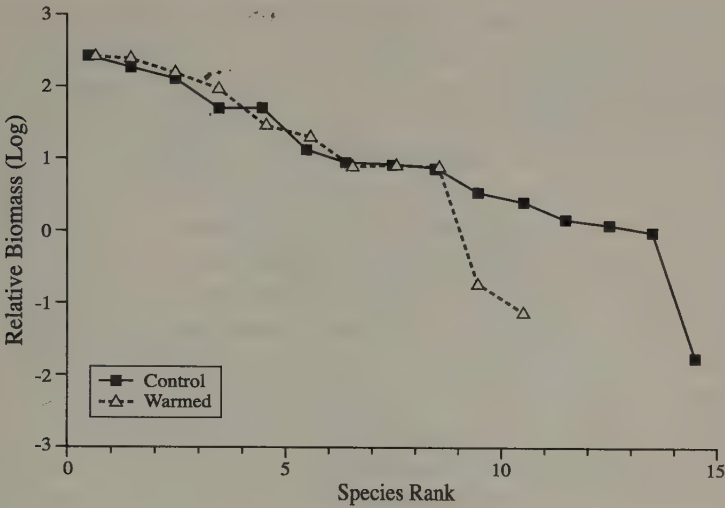


FIGURE 9.3. Biomass of tundra plants plotted as a function of the decreasing rank of species importance in experimental plots in the tundra of Alaska. Experimental plots were warmed, whereas control plots received no manipulative treatment. From Chapin et al. (1995).

experiment produced a striking precocious bloom of Canada mayflower (*Maianthemum canadense*). At Harvard Forest, soil warming accelerated the development of herbaceous species, but it lowered the species richness in treated plots over a three-year period (Farnsworth et al. 1995). Other soil warming experiments resulted in changes in the composition of soil microbial communities (Harte et al. 1996; Zogg et al. 1997; Andrews et al. 2000), consistent with observations of greater soil CO₂ efflux and nitrogen mineralization in heated plots (Peterjohn et al. 1994; Rustad and Fernandez 1998; Lukewille and Wright 1997).

Moisture

Predicted changes in the global distribution and abundance of precipitation as a result of greenhouse warming of Earth's climate are much less certain than the predicted changes in temperature. Most global models suggest greater overall precipitation, owing to a general stimulation of the hydrologic cycle by higher temperatures (Mitchell et al. 1990, p. 138). However, several models suggest that during the transient period of global warming, there will be an increase in the extent and severity of midcontinental droughts (Rind et al. 1990).

Moisture availability certainly affects the distribution of plants and animals, and changes in the abundance and seasonal distribution of precipitation

are likely to produce dramatic changes in species abundance in many areas. In 1988, severe drought reduced the density of birds by 61 percent in the northern Great Plains, but nearly complete recovery was seen in the next year, which had normal rainfall (George et al. 1992). A long-term increase in temperature or a decline in precipitation in the prairies of North America would surely be followed by a decline in the abundance of waterfowl (Poiani and Johnson 1991; Bethke and Nudds 1995; Sorenson et al. 1998), whereas increasing precipitation might expand their habitat.

In semiarid regions, the latitudinal and elevational distribution of vegetation may be more closely correlated with regional gradients in soil moisture than with temperature (Barton and Terri 1993; Hogg 1994; Tucker et al. 1994; Allen and Breshears 1998). During a warm, dry period of the mid-Holocene (~6,000 years ago), prairie and woodland vegetation in central North America expanded eastward, replacing forest (McAndrews et al. 1966; Clark, Grimm et al. 2001). Conversely, if future global warming is accompanied by greater rainfall, forest vegetation may spread to lower, drier elevations, as seen in the western Great Basin during the Pleistocene (DeLucia and Schlesinger 1990).

Examining the climate record for semiarid southern New Mexico, Neilson (1986) suggested that a shift in rainfall from summer to winter aided the expansion of arid-land shrubs, such as creosotebush and mesquite (*Prosopis glandulosa*), at the expense of warm-season grasses such as black grama (*Bouteloua eriopoda*). Brown et al. (1997) drew similar conclusions from long-term field studies in the Chihuahuan Desert in southeastern Arizona. Other factors, such as overgrazing, rising CO₂, and fire suppression may also be involved, but this change in community composition is associated with a loss of species diversity (figure 9.4).

Summary and Research Needs: Climate Changes

The predicted future changes in temperature and moisture associated with a greenhouse warming of Earth's atmosphere are likely to cause dramatic shifts in the distribution of plants and animals (Iverson and Prasad 1998). The climate changes will occur within a century. We know relatively little about the comparative dispersal ability of species, but to the extent that differentials exist, some species with poor dispersal ability may disappear, while the remaining species may be found in new assemblages for which there are no modern analogs (Iverson and Prasad 1998). To the extent that species have evolved in long-term associations with their neighbors, losses of biodiversity may cascade from low to higher trophic levels (Visser et al. 1998; Petchey et al. 1999). For instance, changes in the distribution and abundance

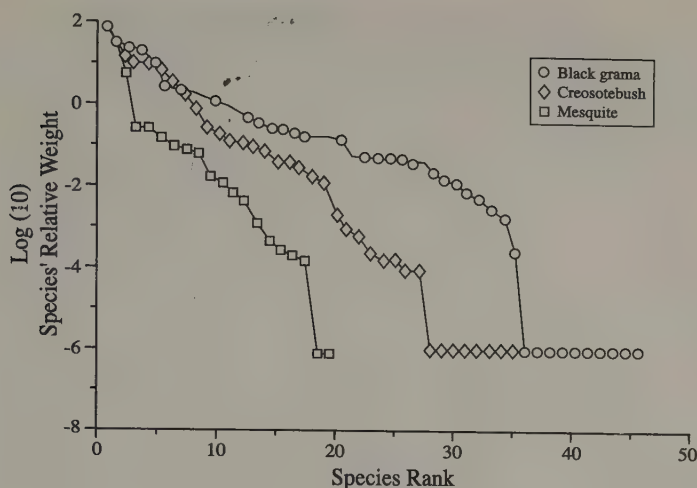


FIGURE 9.4. Plant species diversity in black grama grasslands, and in creosotebush and mesquite shrublands in southern New Mexico. From L. F. Huenneke (unpublished).

of animals may depend more on changes in vegetation than on changes in the thermal conditions of the animals per se (Johnston and Schmitz 1997).

Conservation biology will benefit from more studies in which temperature and moisture are manipulated to study their effects on species diversity. These should be whole-ecosystem studies—not of warming of the soil alone. Long-term experiments are essential; in short-term experiments, warming may lead to a loss of native species at a rate greater than the rate of immigration of species that might flourish at warmer temperatures (table 9.1). Also, in nature, species are often more responsive to extreme events, whereas warming experiments typically impose only changes in mean annual temperature (for a welcome exception, see White et al. 2000). Future workers may wish to design field studies of species response to unusual, rather than altered mean, conditions. Experiments that impose warming should focus on high-latitude ecosystems, where climatic warming is projected to be greatest. Experiments that impose changes in moisture—by either additions or exclusions of rainfall—are most needed in semiarid ecosystems, where shifts in the moisture regime are likely to have critical effects on the persistence of species. These studies should also examine changes in the seasonal distribution and interannual variability of moisture, perhaps following the model used by Reynolds et al. (1999) for field experiments in the Chihuahuan Desert.

TABLE 9.1. Whole-Ecosystem Experiments Examining Changes in Plant Biodiversity in Response to Anticipated Global Environmental Change

Experimental Perturbation Biome	Biodiversity Response	Reference
Ecosystem warming	Decline	Harte and Shaw (1995)
Alpine tundra	No change	Price and Waser (2000)
Ecosystem warming	Decline	Chapin et al. (1995)
Arctic tundra		
Soil warming	Lower richness	Farnsworth et al. (1995)
Temperate forest		
High CO ₂	No change in richness	Leadley et al. (1999)
Temperate grassland	Higher equitability	
High CO ₂	Higher richness	Potvin and Vasseur (1997)
Temperate grassland	Higher equitability	
Nitrogen deposition	Decline	Wedin and Tilman (1996)
Temperate grassland		
Nitrogen deposition	Decline	Bakelaar and Odum (1978)
Temperate field		
Fertilization	Lower richness	Kempton (1979)
Temperate fields	Lower equitability	

Rising Carbon Dioxide

During the last 420,000 years, the concentration of atmospheric carbon dioxide dipped below 200 ppm during each of the Pleistocene ice ages (Petit et al. 1999). At the end of the last continental glaciation, it increased to 270 ppm, where it remained with minor fluctuations until the beginning of the Industrial Revolution. The rapid increase to the current level of 360 ppm, due to the combustion of fossil fuels and deforestation of the tropics, is unprecedented in the geologic history of Earth (Schlesinger 1997). By the year 2050, the global CO₂ concentration is expected to reach 560 ppm (Schimel et al. 1995).

Carbon dioxide is the primary raw material for photosynthesis, and changes in its concentration have direct effects on the growth of plants, leading to changes in competitive abilities and potential impacts on biodiversity. For example, the decreased photosynthetic rate of C3 plants relative to that of C4 plants at low atmospheric CO₂ concentrations is believed to have triggered the expansion of C4 plants at the end of the Miocene, approximately seven million years ago (Cerling et al. 1993, 1997). When grown at low CO₂ concentrations, replicating conditions during the last continental glaciation (18,000 years ago), the C3 weed *Abutilon theophrasti* was unable to reproduce,

while C4 plants flourished in the same conditions (Dipperry et al. 1995). The rise in C3 plants during the Holocene has been attributed to the rise in atmospheric CO_2 at the end of the last glaciation, which increased their competitive ability (Cole and Monger 1994). In semiarid regions, a further decline in the C4 grasses during the past century may be due to a greater competitive ability of C3 shrubs and savannah trees under the rising concentrations of atmospheric CO_2 (Johnson et al. 1993; Polley et al. 1994).

In greenhouse experiments, elevated atmospheric CO_2 generally enhances plant productivity, with an average growth increase of 30–40 percent at 2X CO_2 and optimal growth conditions (Poorter 1993; Curtis and Wang 1998). In nature, where plant growth is often limited by nutrients, light, and/or soil moisture, the effect of CO_2 is smaller (Bazzaz 1990; DeLucia et al. 1999) and decreases with long-term exposure (Hattenschwiler et al. 1997; Idso 1999). Accelerated plant development with elevated CO_2 may explain the diminished growth response after long-term exposure (St. Omer and Horvarth 1983; Tissue, Thomas, and Strain 1997; Reid and Fiscus 1998; Ward et al. 2000). In their natural habitat, plants are subject to herbivory, competition, and mutualisms, so the effects of altered CO_2 on one plant are at least partly a function of its effect on neighboring plants, animals, and soil microbes.

Forest Ecosystems

In forests, a few studies show that early-successional, shade-intolerant “pioneer” species benefit from elevated CO_2 relative to shade-tolerant competitors, especially when grown under the low-light and/or low-nutrient conditions that typify most forest understories (Hattenschwiler and Korner 1996; Brown and Higginbotham 1986). Several physiological mechanisms explain how plants may require less light when grown under elevated CO_2 (Hirose et al. 1996; Pearcy and Bjorkman 1983). These experiments suggest that early-successional growth forms may retain their dominance and persist for longer periods under elevated CO_2 conditions. Since species diversity tends to increase during succession (Peet 1992), a delay in the successional process might be expected to decrease regional biodiversity, especially as mature forests become increasingly rare in human-dominated landscapes.

Pioneer (early-successional) species typically have higher innate relative growth rates than later-successional species (Bazzaz and Pickett 1980; Walters and Reich 1996, 2000). Growth enhancement by CO_2 fertilization is twice as great in fast-growing as in slower-growing species (Ackerly and Bazzaz 1995; Poorter 1998). Among slow-growing species, however, differences in relative growth rate are not correlated with the CO_2 -growth response (Reid and Strain 1994). Thus, fast-growing, “weedy” plants may benefit most from future levels of atmospheric CO_2 , leading to an increase in

early-successional communities and a reduction in overall species diversity (Bazzaz 1996).

Many field studies, however, suggest the opposite conclusion. These studies show that shade-tolerant, later-successional tree species benefit from elevated CO_2 more than early-successional trees (Kubiske and Pregitzer 1996; Bazzaz et al. 1990; Williams et al. 1986), even when the seedlings are grown under low-light, low-nutrient, "forestlike" conditions (Bazzaz and Miao 1993; Hattenschwiler and Korner 2000). Various traits associated with shade tolerance may explain the tendency for these species to show a strong CO_2 growth response (Kerstiens 1998).

Field studies in the Duke Forest Free-Atmosphere Carbon Dioxide Enrichment (FACE) site, where elevated (560 ppm) and ambient (360 ppm) CO_2 conditions were maintained in a fifteen-year-old (in 1996) loblolly pine (*Pinus taeda*) forest, support the prediction that later-successional, shade-tolerant trees will be favored by future CO_2 levels (figure 9.5). In the second year of CO_2 treatment, seedlings of shade-tolerant understory trees grew 90 percent larger under elevated CO_2 compared to the ambient treatment. Seedlings of shade-intolerant and intermediately tolerant understory trees showed no significant CO_2 growth effects. These results suggest that during forest regrowth later-successional species will be favored and elevated CO_2 may increase species diversity.

In addition to different responses by species of differing shade tolerances and growth rates, different growth forms exhibit distinct growth responses to CO_2 enrichment. For example, vines, due to their lower carbon requirements for support tissues, typically exhibit a greater response to elevated CO_2 than trees (Bazzaz 1996; Sasek 1985). In addition, vines allocate more of their photosynthate to increase the photosynthetic area, causing a further enhancement in growth. In the Duke Forest FACE experiment, the understory vine poison ivy (*Toxicodendron radicans*) had a 71 percent increase in growth under elevated CO_2 when protected from mammalian herbivory. The growth enhancement of this vine far exceeds the 25 percent growth increase of the canopy trees (DeLucia et al. 1999).

Earlier work showed large growth enhancements (135 percent and 51 percent increases, respectively) when the exotic vines Japanese honeysuckle (*Lonicera japonica*) and kudzu (*Pueraria lobata*) were grown at elevated CO_2 under optimal greenhouse conditions (Sasek and Strain 1988, 1989, 1991). Both species are pernicious weeds in the southeastern United States. Sasek and Strain (1991) found only a 44 percent increase in the growth of the native, coral honeysuckle (*L. sempervirens*) at high CO_2 —far less than that of the invasive, congeneric competitor. Characteristics of successful exotic species (e.g., fast growth rate and low resource requirements) may also be associated

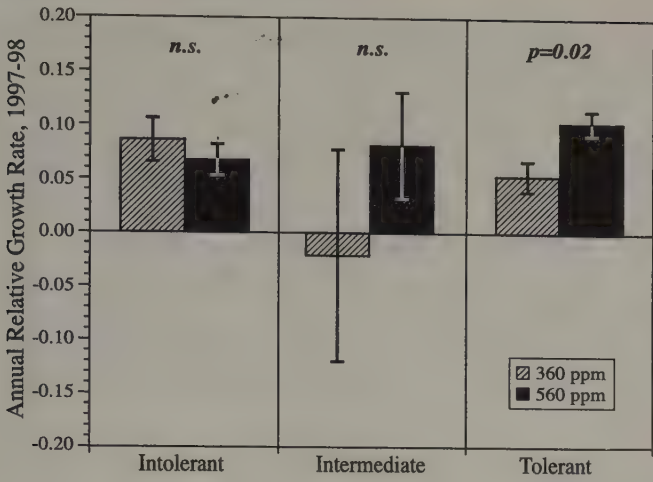


FIGURE 9.5. Relative growth rate of classes of tree seedlings in the Duke Forest Free-Air CO₂ Enrichment (FACE) experiment, in control plots and plots receiving a continuous 200-ppm supplement of CO₂. Seedlings of shade-tolerant species showed significant higher growth at elevated CO₂ ($P < 0.02$), while other species groups showed no effect. These growth rates were calculated from plants showing positive growth increments in uncaged plots, subject to mammalian herbivory. From J. E. Mohan (unpublished data).

with strong CO₂ growth responses. *L. japonica* has been linked to reduced tree recruitment and increased sapling mortality in eastern forests (Sasek 1985; Dillenburg et al. 1995) and is predicted to expand northward as a consequence of global warming (Sasek and Strain 1990). If vines become more competitive with elevated CO₂, future forest composition and species diversity will certainly be impacted.

In addition to the dramatic response of vines, tree species capable of harboring symbiotic nitrogen-fixing bacteria often show large increases in growth in response to elevated CO₂ (Arnone and Gordon 1990; Norby 1987; Thomas et al. 1991; Tissue, Megonigal, and Thomas 1997). Higher rates of plant photosynthesis at high CO₂ may allow N-fixing species to allocate additional carbohydrate to support their N-fixing symbionts and to avoid nutrient deficiencies that could otherwise result from accelerated growth.

Grassland Ecosystems

The effects of elevated atmospheric CO₂ on species diversity have also been studied in grassland ecosystems. Owensby et al. (1999) reported that C3 grasses declined and C3 forbs increased during an eight-year study of an

ungrazed tallgrass prairie exposed to elevated CO_2 . Although Leadley et al. (1999) found no CO_2 effect on the number of species in their four-year study of calcareous Swiss grassland, rare species became more abundant, so the overall diversity of the community increased slightly. In a three-year study of a Canadian pasture, Potvin and Vasseur (1997) observed higher species richness, increased equitability, and reduced extinction rates under elevated CO_2 , but the resulting boost in species diversity favored pioneer species at the expense of later-successional species. Interestingly, in several studies, N-fixing species showed particularly large increases in abundance (Luscher et al. 1996; Leadley et al. 1999; Vasseur and Potvin 1998; Warwick et al. 1998) and changes in the population of N-fixing symbionts (Montealegre et al. 2000).

Higher Trophic Levels

Bezemer and Jones (1998) reviewed a large and growing literature on changes in the performance of insects feeding on plants grown under elevated CO_2 . In nearly all cases, plant tissues grown at high CO_2 have lower nitrogen and higher carbohydrate concentrations, stimulating greater consumption by "leaf chewing" species (Docherty et al. 1996). Plants with the highest growth response to high CO_2 show the greatest increase in leaf carbon content, whereas slow-growing species often show increases in leaf defensive compounds as well as carbon (Lindroth, Kinney, and Platz 1993). The abundance of "phloem feeders" often increases when plants are grown at high CO_2 (Bezemer and Jones 1998), presumably due to higher levels of soluble carbohydrate available to support those insects. The changes in plant and insect populations are likely to mediate most changes in the abundance of vertebrates in response to rising CO_2 , because there is no evidence of direct physiological effects of the predicted, elevated future CO_2 concentrations.

Soil Ecosystems

Rising concentrations of atmospheric CO_2 are unlikely to have a direct impact on soil organisms, which normally live in an environment of high CO_2 . However, these organisms respond to increases in the input of labile carbon and plant residues to the soil (Sadowsky and Schortemeyer 1997; Jones et al. 1998; Degens et al. 2000), and the responses of decomposers may, in turn, affect plant growth (Naeem et al. 2000). Zak et al. (1996, 2000) reported higher microbial biomass but no apparent change in microbial community composition in soils used to grow poplar (*Populus grandidentata*) at elevated CO_2 (cf. Bruce et al. 2000). In contrast, using the same techniques, Ringelberg et al. (1997) found changes in the composition of microbial com-

munities under white oak (*Quercus alba*). When grass species were grown at high CO_2 , there was little change in soil microbial diversity (Hodge et al. 1998), although the number of N-fixing symbiotic bacteria increased in one study (Schortemeyer et al. 1996). Yeates et al. (1999) found a general decrease in nematode diversity and abundance, but an increase in the abundance of bacteria-feeding nematodes, in soils of a plant community exposed to high CO_2 near hydrothermal vents in New Zealand. On the other hand, Klironomos et al. (1996) found a large increase in the density of soil microfauna under desert shrubs grown at high CO_2 in fertile conditions. Zaller and Arnone (1999) found no effect of CO_2 enrichment on earthworm communities in calcareous Swiss pastures.

Mycorrhizae, the symbiotic fungi that enhance the nutrient uptake by higher plants, often increase when plants are grown under elevated CO_2 and low soil fertility (DeLucia et al. 1997; Walker et al. 1995; Klironomos et al. 1997). Klironomos et al. (1998) found that plant growth at elevated CO_2 affected mycorrhizal colonization, spore production, and hyphae growth, with different responses among four fungal varieties. Godbold et al. (1997) also found that elevated CO_2 affected mycorrhizal colonization, with the response depending on both the type of fungi and the species of tree that formed the symbiosis. Clearly, more work is needed to define the general response of mycorrhizal communities to the growth of their host plants at high CO_2 .

Marine Ecosystems

The continuing rise in atmospheric CO_2 will lead to a drop in seawater pH, as apparently occurred during the early Miocene, 21 million years ago (Spivack et al. 1993). Because the formation of aragonite—the primary carbonate mineral of corals—declines at lower seawater pH, decalcification may lead to the bleaching and degradation of coral reefs in many tropical areas. The formation of biogenic aragonite, and thus coral reefs, is expected to decrease by 14–30 percent by the year 2050, as a direct result of rising atmospheric CO_2 (Kleypas et al. 1999; Leclercq et al. 2000). Thus, rising CO_2 may act in concert with rising temperature to increase the bleaching and degradation of coral reefs.

Marine phytoplankton are typically limited by the availability of nitrogen and phosphorus in seawater, so the growth of phytoplankton shows little response to changes in atmospheric CO_2 content. Nevertheless, some studies suggest both higher oceanic primary production as a result of increases in CO_2 and differential species' responses that might affect biodiversity (Hein and Sand-Jensen 1997; Raven 1994).

Summary and Research Needs: Rising CO₂

A limited number of field observations and experiments suggest that rising concentrations of atmospheric CO₂ will affect the composition and structure of ecological communities. Many, but not all, studies suggest that plant species with high innate growth rates will benefit from elevated CO₂, potentially lowering regional biodiversity. The competitive relations of species will be determined by the effect of CO₂ on plant photosynthesis, water relations, and nutrient uptake, and the translation of these effects to higher trophic levels. The potential for rapid evolution in response to elevated CO₂ is suggested by high intraspecific variation in plant response to CO₂ (Curtis et al. 1996; Ward and Strain 1997; Andalo et al. 1998; DeLucia et al. 1997; Wayne and Bazzaz 1995, 1997) and by the results of selection experiments extending over several generations of short-lived plants (Tousignant and Potvin 1996; Ward et al. 2000). However, the evolutionary response of trees and other long-lived species is likely to lag behind the large rise in atmospheric CO₂ expected during this century.

Despite their high cost, Free-Air CO₂ Enrichment experiments provide the greatest insight into whole-ecosystem changes in ecosystem processes and species diversity that are likely to accompany the rise of CO₂ in Earth's atmosphere. The greatest insight will stem from FACE experiments that operate for a decade or more, and those in which the high CO₂ treatment is examined in conjunction with other factors, especially changes in nitrogen input. The response of biodiversity to CO₂ enrichment should be carefully examined in semiarid ecosystems, where changes in plant water-use efficiency in response to high CO₂ may have dramatic changes in the availability of soil water and the competitive ability of some species.

Nitrogen Availability and Acidification

The biota of most terrestrial and marine ecosystems has evolved in a state of chronic nitrogen deficiency, so changes in the availability of nitrogen would be expected to have dramatic effects on plant community structure. Through the production of synthetic nitrogen fertilizer, humans have roughly doubled the annual input of available nitrogen to the earth's surface, causing large increases in the concentration of nitrogen in surface and ground waters (Vitousek et al. 1997). Excessive nitrogen in runoff has caused losses of species in a variety of wetland and coastal habitats, the most well known being the loss of fish and shellfish in the "dead zone" in the Gulf of Mexico (Turner and Rabalais 1991; Rabalais et al. 1996). In coastal marine waters, human inputs of nitrogen have shifted nutrient limitation from nitrogen to silicon, resulting in shifts in the relative abundance of phytoplankton species (Turner and Rabalais 1994; Justic et al. 1995). Atmospheric

transport of reactive nitrogen compounds (e.g., ammonia [NH_3] and nitric oxide [NO_x]) carries human perturbation of the nitrogen cycle to all regions of the earth (Holland et al. 1997), as seen in ice-core records of nitrogen deposition in Antarctica (Mayewski and Legrand 1990) and Greenland (Mayewski et al. 1986). In the Netherlands, where deposition of nitrogen from the atmosphere is perhaps twenty-five times higher than one hundred years ago, formerly diverse pastures are now dominated by pure stands of bracken fern (*Brachypodium*), and *Calluna* heathlands have been replaced by depauperate grasslands of *Deschampsia* and *Molinia* (Heil and Diemont 1983). These community changes can be replicated by experimental additions of nitrogen fertilizer to field plots (Bobbink 1991; Willems and Peet 1993).

Nearly all field experiments show a decline in species diversity with nutrient enrichment (e.g., Hurd et al. 1971; Huenneke et al. 1990; Mun and Whitford 1989). Austin and Austin (1980) found lower species richness and equitability in experimental communities of grassland plants, resulting in changes in dominance-diversity curves that resemble those from the Parkland field plots (figure 9.1). Wedin and Tilman (1996) report over 50 percent reduction in plant diversity in field plots receiving nitrogen fertilizer over a twelve-year period. Bakelaar and Odum (1978) also show lower richness and equitability among the weed species of fertilized fields (figure 9.6). Although these changes in diversity were similar to those seen during ecosystem retrogression, Bakelaar and Odum note that the species that remained were those normally associated with later-successional stages. Ecologists have ample theory to explain these observations: the higher species diversity in natural communities persists when resources are low, so that each species is limited by a different resource (Levin 1970; Rosenzweig 1971; Tilman 1982). Any addition of a limiting resource to such a community will lead to the dominance of the species that can usurp that resource most effectively. Plant species with high inherent relative growth rates may benefit most from the synergistic effects of high CO_2 and soil nitrogen availability (Poorter 1998). Surprisingly, despite observations of higher plant production and lower plant diversity in fertilized, versus unfertilized, fields, Hurd et al. (1971) found an equal or higher diversity of herbivorous and carnivorous arthropods on the plants in fertilized fields.

Inasmuch as NO_x is removed from the atmosphere by reactions yielding nitric acid (HNO_3) in rainfall, human perturbations of the global nitrogen cycle may also be associated with a greater regional occurrence of "acid rain." Conversely, in some areas, anthropogenic emissions of ammonia (NH_3) may reduce the acidity of rainfall (Schlesinger 1997). The effects of acid rain on plants, fish, and amphibians are well known (Pough 1976; Schindler 1988).

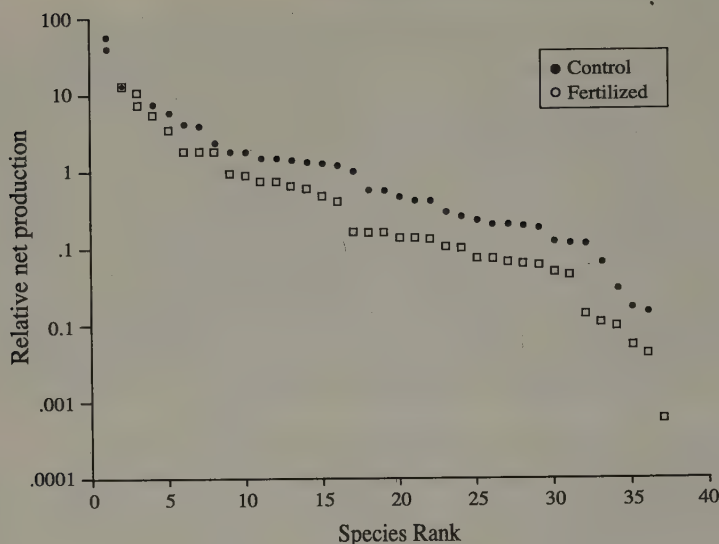


FIGURE 9.6. Relative net production of plants in control and fertilized plots in an abandoned field in Georgia, plotted as a function of the relative importance of species in the ecosystem. From Bakelaar and Odum (1978).

Air pollution and acid rain reduce plant species diversity and equitability in forest ecosystems (McClenahen 1978; Freedman and Hutchinson 1980). In many cases, the effect of acid rain on trees is mediated by changes in soil chemistry, rather than a direct effect on leaf tissues (Schlesinger 1997; Blake et al. 1999). Acid rain also causes indirect effects on higher trophic levels. For example, in the Netherlands, reproduction of the great tit (*Parus major*) is poor in forests subject to acid rain, owing to a decline in the abundance of snails, which are the main source of calcium for this bird's eggshells (Graveland et al. 1994).

Following the implementation of stringent air quality standards that reduced the emission of SO_2 in many developed countries, many aquatic ecosystems have recovered rapidly from previous, higher levels of acid deposition (Tipping et al. 1998; Stoddard et al. 1999). At the same time, nitric acid has become an increasingly important component of the anthropogenic acidity in rainfall, and high concentrations of NO_x are also associated with the formation of tropospheric ozone, which is a serious regional air pollutant.

Summary and Research Needs: Nitrogen Cycle

Humans will respond to the demand to feed ten billion of their own number, so the use of synthetic nitrogen fertilizer, and its inadvertent release to the environment, will undoubtedly increase during the next century. We believe

that this human perturbation of the global nitrogen cycle will emerge as a serious threat to global biodiversity.

Field experiments that manipulate the availability of nitrogen are often easier to perform than those aimed at altering the temperature, moisture, or CO₂ regime. Experiments to examine changes in ecosystem processes (e.g., McGill et al. 1997) could easily be maintained for long enough periods to also examine changes in biodiversity. Additional experiments should examine changes in biodiversity in response to the simultaneous exposure of ecosystems to high nitrogen and high CO₂. Special attention should be paid to the response of exotic species in nitrogen-rich habitats. It will be critical to establish large-scale experiments that evaluate the link between the nitrogen loading of fresh waters and subsequent changes in biodiversity and ecosystem function of the estuaries and coastal waters into which they drain. A recent analysis suggests that nutrient additions increase the production of phytoplankton in pelagic waters, without causing large changes at higher trophic levels (Micheli 1999).

Tropospheric Ozone

The photochemical production of ozone (O₃) from volatile organic carbon (VOC) compounds now dominates the ozone budget of the lower atmosphere—the troposphere (Levy et al. 1997). In urban areas, the reaction is catalyzed by high concentrations of nitrogen oxide gases derived from fossil fuel combustion. Low concentrations of NO_x formerly limited the production of ozone in most rural areas, but increasing atmospheric dispersal of NO_x from human activities (e.g., Cooper and Peterson 2000) and emissions from agricultural soils (Davidson et al. 1998) now cause regional ozone pollution in many of these areas as well (Chameides et al. 1994). Since the beginning of the Industrial Revolution, emissions of VOC and NO_x have doubled the O₃ background concentration (Fowler et al. 1998). Ozone concentrations in the lower atmosphere, averaging 10 nl l⁻¹ from 1876 to 1910, are now up to 25–30 nl l⁻¹ (Volz and Kley, 1988). Ozone concentrations are projected to increase 15 percent by the year 2035 (Thompson et al. 1990), approaching the critical 40 nl l⁻¹ threshold level for vegetation (Fuhrer et al. 1997). High O₃ concentrations are now reported in remote areas of the South Pacific (Jiang and Yung 1996), in South America, and in Africa (Fishman et al. 1990). Emissions of NO_x from ships may more than double the background concentration of tropospheric O₃ over the North Atlantic and Pacific oceans (Lawrence and Crutzen 1999). Thus, the toxic effects of ozone are potentially a global problem, in both urban and rural areas. In forests, conifers appear more resistant to episodic O₃ exposures than broadleaf species—deciduous trees being the most sensitive (Reich 1987; Chappelka and

Samuelson 1998; Shärky et al. 1998). Black cherry (*Prunus serotina*) is among the most sensitive species in the United States (Rebbeck 1996), and in Europe, birch, aspen, and poplar are very sensitive to ozone damage (Shärky et al. 1998). Understory seedlings and saplings appear to incur less damage from O_3 than do canopy trees (Samuelson and Kelly 1997). In grasslands, fast-growing, invasive, and early-successional species are more sensitive to ozone than the slow-growing, late-successional species (Reiling and Davison 1992; Bungener, Nussbaum, et al. 1999).

A decrease in the cover of forbs is reported for grasslands exposed to O_3 on both acid (Ashmore and Ainsworth 1995) and calcareous (Ashmore et al. 1995) soils. In European grasslands, legumes are more sensitive to O_3 than other herbs and grasses (Fuhrer et al. 1994; Nebel and Fuhrer 1994; Warwick and Taylor 1995; Bungener, Balls, et al. 1999). A reduction in the legume clover with chronic O_3 exposure was associated with increases in grasses in the United States (Bennett and Runeckles 1977; Rebbeck et al. 1988). Davison and Barnes (1998) suggested that this sensitivity of legumes to O_3 could reduce N fixation and thus ecosystem nutrient availability.

Although these studies suggest species-specific responses to tropospheric O_3 , few studies have addressed the effect of O_3 on species diversity per se. Westman (1979) reported that a decline in the biodiversity of coastal sage scrub was correlated with the concentration of airborne oxidants, which included O_3 (figure 9.7). Barbo et al. (1998) reported lower species diversity in an early-successional community exposed to elevated O_3 than in a similar community grown in charcoal-filtered air. Barnes et al. (1999) suggest that in many areas species that are sensitive to ozone have already been eliminated from natural communities. Reductions in biomass and acceleration of plant development and leaf senescence during chronic O_3 exposures (Pell et al. 1997; Reid and Fiscus 1998) are likely to decrease the reproductive potential of sensitive species. Ample examples of such reduced biomass and seed yield exist for crop species (e.g., reviews by Miller 1988; Heagle 1989). In natural communities, such changes are likely to alter species dominance and diversity.

Leaf conductance, which controls the uptake of CO_2 and O_3 by vegetation, is a main determinant of potential O_3 damage (Heath 1994). In studies examining a range of species, those most sensitive to O_3 had high stomatal conductances (Reich 1987; Nebel and Fuhrer 1994; Bungener, Balls, et al. 1999). Similarly, the greater O_3 sensitivity of canopy trees than of seedlings is associated with a greater leaf conductance in the trees (Samuelson and Kelly 1997). Chappelka and Samuelson (1998) suggest that stomatal conductance may be a good index for ozone tolerance in eastern tree species. The ranking of O_3 tolerance among conifers and broadleaf shade-tolerant and intolerant trees is

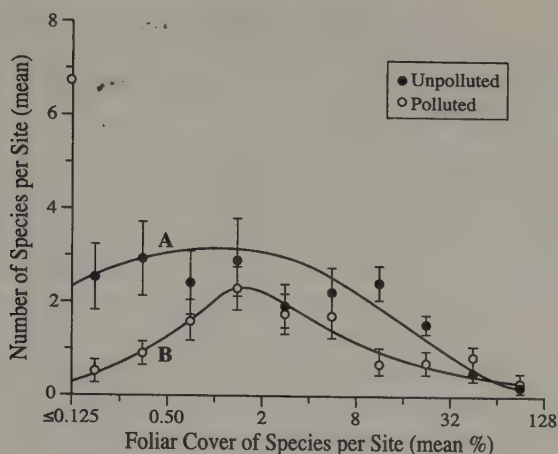


FIGURE 9.7. Lognormal distributions of species importance in polluted (B) and unpolluted (A) plots in the coastal sage scrub of Southern California. Reprinted with permission from Westman (1979). Copyright © 1979 American Association for the Advancement of Science.

correlated with differences in leaf conductance (Reich 1987). In addition, greater O_3 tolerance has been related to lower stomatal density (a determinant of leaf conductance) in comparisons among ash populations (Bennett et al. 1992), pine species (Evans and Miller 1972), and herbaceous plants (Evans et al. 1996).

Natural selection for O_3 tolerance has been observed in trees and herbs. A comparison of *Plantago major* populations from regions differing in O_3 concentration and climate suggests that O_3 is a major selection factor for O_3 -resistant genotypes (Lyons et al. 1997). Whitfield et al. (1997) showed that genetic variation for O_3 resistance resulted in a resistant *Plantago* population, with lower leaf conductance, after four generations of selection. In two common garden experiments, Berrang et al. (1989) reported similar selection for O_3 resistance in poplar (*Populus tremuloides*) clones from several areas differing in O_3 concentration.

Little is known about O_3 effects on higher trophic levels. Studies of plant-animal interactions report higher rates of insect herbivory on O_3 -injured than on noninjured leaves (Jones et al. 1994; Chappelka et al. 1997). Growth rates of spider mite populations are higher on clover (*Trifolium repens*) exposed to O_3 than on clover grown in charcoal-filtered air (Heagle et al. 1994). Feeding on O_3 -injured leaves had no effect on gypsy moths (Lindroth, Reich et al. 1993) or aphids (Jones et al. 1994), but it decreased a beetle population (Jones et al. 1994). The increased herbivory on O_3 -damaged tissue is likely to impact the long-term growth and survival of plants, and potentially

their herbivores. Changes in plant diversity and community structure as a result of exposure to O_3 will likely affect food sources and protective cover for other trophic levels, including microbial communities in the soil (Islam et al. 2000).

Studies on the interactive effects of pollutant O_3 and CO_2 suggest that O_3 damage is ameliorated by elevated atmospheric CO_2 . For example, photosynthesis is higher in crop plants exposed to a combination treatment of elevated CO_2 and O_3 than in plants exposed only to O_3 (McKee et al. 1995; Reid and Fiscus 1998). Similar results are reported for trees (e.g., beech [*Fagus sylvatica*], Grams et al. 1999; and Scots pine [*Pinus sylvestris*], Kellomäki and Wang 1997a, b). These studies also report a decrease in leaf conductance in a combined treatment of elevated CO_2 and O_3 . Reduced flux of O_3 into the leaves because of reduced leaf conductance with elevated CO_2 partially explains the amelioration response (McKee et al. 1995; Fiscus et al. 1997).

Although the interactive effects of ozone and CO_2 on leaf physiology have been studied in trees and herbs, studies of their interactive effects on growth are limited to crop species (e.g., wheat [McKee et al. 1997; Mulholland et al. 1997, 1998], corn [Rudorff et al. 1996], and soybean [Fiscus et al. 1997; Miller et al. 1998]). Nevertheless, the similar physiological responses of crops and trees suggest that the growth of native species will also be ameliorated. A comparison of six perennial species, including trees and C3 and C4 grasses, suggests that amelioration may be widespread among perennials (Volin et al. 1998). However, the increase in growth with elevated CO_2 in O_3 -fumigated air does not always translate into increased reproductive potential (Fiscus et al. 1997; Reid and Fiscus 1998). McKee et al. (1997) found no amelioration of wheat seed yield with elevated CO_2 when exposed to O_3 -fumigated air, whereas Fiscus et al. (1997) found such an amelioration of seed yield in soybean. These authors further speculate that the enhancement in yield often reported with elevated CO_2 might be an artifact of lower damage from O_3 pollution. A review of the interactive effects of elevated CO_2 and O_3 on crop seed yield supports this hypothesis (Fiscus et al. 2000), but further investigations are needed.

Summary and Research Needs: Tropospheric Ozone

The effect of ozone on biodiversity resembles that of many other toxic effluents. The decrease in growth and seed set with O_3 exposure reduces plant biomass and species composition, which, in turn, adversely affects higher trophic levels. Differential sensitivity among species is likely to result in changes in community composition in regions of high exposure, potentially decreasing biodiversity. Unfortunately, no field experiments have examined changes in biotic diversity in natural systems with simultaneous exposure to

both high CO₂ and O₃. The evidence to date suggests that interactive effects of O₃ and CO₂ will alter predictions based on responses to each gas separately. Field experiments, using the approach of Free-Air CO₂ Enrichment, will offer important insight into the changes in biodiversity expected in ecosystems that are exposed to O₃ for long periods, including acute short-term exposure to high concentrations. These O₃ studies should be designed to examine the interaction of O₃ with CO₂ and other environmental factors that are changing globally.

Increasing UV-B Radiation

While high concentrations of ozone in the troposphere have potentially toxic effects, high concentrations of ozone in the upper atmosphere—the stratosphere—protect the world's biota from potentially damaging effects of the sun's ultraviolet radiation (UV-B). Increasing UV-B radiation at the earth's surface has accompanied the appearance of the "ozone hole" over Antarctica (McKenzie et al. 1999) and losses of stratospheric ozone over temperate regions (Correll et al. 1992; Kerr and McElroy 1993). Increased UV-B radiation may affect the genome stability of plants (Ries et al. 2000).

UV-B radiation is absorbed by water, greatly attenuating its effects at depth. Nevertheless, greater UV-B radiation may already be reducing phytoplankton photosynthesis (Behrenfeld et al. 1993) and productivity in Antarctic waters (Smith et al. 1992; Neale et al. 1998). Various marine species are known to have differential sensitivity to UV-B radiation (Smith et al. 1992), but the effects of UV-B radiation on each species may be mediated by its seasonality and the vertical mixing of ocean waters (Hunter et al. 1981). McMinn et al. (1994) could find no evidence for unusual changes in the species composition of diatom communities in Antarctic waters during a recent twenty-year interval.

For land plants, Laakso and Huttunen (1998) note that pine seedlings are sensitive to short-term exposures to elevated UV-B radiation, but evidence for growth reductions in long-term field studies is limited to only one species, loblolly pine (Sullivan and Teramura 1992). Several studies have noted differential sensitivities of land plants to UV-B (Day et al. 1992), and one study found *enhanced* growth of the weed *Oenothera parviflora* in response to elevated UV-B exposure (Cybulski and Peterjohn 1999). Significant differences in the accumulation of UV-B protective flavonol compounds were noted among populations of clover grown in controlled conditions, with stress-adapted populations accumulating the largest amounts (Hoffman et al. 2000). Yakimchuk and Hoddinott (1994) noted that simultaneous exposure to elevated CO₂ and UV-B radiation reduced the seedling growth of three boreal forest species, but less so than exposure to high UV-B alone. Klironomos and

Allen (1995) note changes in the soil microbes associated with sugar maple (*Acer saccharum*) grown with supplemental UV-B.

Caldwell and Flint (1994) reviewed more than three hundred studies of the effects of UV-B radiation on terrestrial ecosystems. They note that studies showing differential species sensitivity have been conducted in controlled conditions (e.g., Gold and Caldwell 1983), but there are no long-term whole-ecosystem studies of the effects of UV-B on species diversity or ecosystem function. Subsequently, Day et al. (1999) reported increased growth of two vascular plants on the Antarctic Peninsula in response to experimental reductions in UV-B. Significantly, they found no interactive effects between UV-B levels and treatments imposing experimental warming. Recently, a one-year field experiment using plastic filters to reduce the high incidence of UV-B radiation on Tierra del Fuego, Argentina, resulted in only minor changes in plant growth in bogs and fens (Searles et al. 1999). Similarly, Norton et al. (1999) and Papadopoulos et al. (1999) report only small changes in artificial grassland communities exposed to ambient and elevated levels of UV-B. One study reports a greater abundance of freshwater algae in response to elevated UV-B, owing to its disproportional deleterious effects on the normal consumers of algal biomass (Bothwell et al. 1994).

Significant media attention has been devoted to studies suggesting that the worldwide decline in amphibian abundance may be related to the effects of increasing levels of UV-B radiation on amphibian embryos (Alford and Richards 1999; Blaustein et al. 1994). Other studies have produced conflicting results (Cummins et al. 1999), and the interaction of UV-B with other environmental factors and species-specific sensitivity is deserving of further study.

Conclusions

We concur with the recent biodiversity assessment that suggests that land use and climate change pose the most serious global threats to biodiversity (Sala et al. 2000). Beyond climate change, humans are causing a variety of changes in the chemistry and physical characteristics of Earth's environment. To the extent that species respond differently to those changes, some species may increase in abundance, while others may decline, leading to global changes in the composition and diversity of ecological communities. Many studies suggest that the responses of natural ecosystems to stress include losses of species and an increasing dominance of a few species that are competitive in the newly established environmental conditions. Studies of past environments confirm losses of species and genetic diversity during periods of environmental change; thus, we expect that global environmental change will lead to losses of biodiversity during this century. Policies to pro-

tect biodiversity from those changes must include international agreements that are successful in reducing the emission of greenhouse gases and pollutant levels of nitrogen and ozone to the environment. The policy-making process should be guided by large-scale, long-term field experiments that validate model projections of changes in biodiversity in response to global environmental change. Priority research areas are listed in box 9.1.

BOX 9.1. Research Priorities for Ecosystem Studies Relevant to Conservation Biology

1. Investigate global climate change, including long-term, whole-ecosystem effects of warming and altered moisture availability, particularly for the Arctic (warming) and desert (moisture).
 - Is the rate of species loss matched by the invasion of new species more suited to the altered environmental conditions?
 - Are alterations of the mean conditions (temperature and precipitation) more or less important to species persistence than alterations of extreme conditions?
2. Investigate rising carbon dioxide, including long-term, whole-ecosystem effects of high CO₂ on ecosystem function for all ecosystems, but particularly for localities with simultaneous exposure to high N deposition and O₃ and in desert ecosystems, where the effects of CO₂ and moisture availability interact.
 - Is there evidence for rapid selection of genotypes favored for growth at high CO₂?
 - How do simultaneous exposures to high temperature, nutrient additions, and O₃ affect ecosystem response to high CO₂?
3. Investigate the nitrogen cycle, including long-term, whole-ecosystem experiments with enhanced levels of nitrogen input, particularly for temperate grasslands, temperate forests, and estuarine and coastal ecosystems.
 - What is the effect of chronic levels of high N input on the biodiversity of terrestrial ecosystems?
 - Is the success of exotic species enhanced under high N inputs?
 - What is the effect of high N inputs on trophic level structure in estuarine systems?
4. Investigate tropospheric ozone, including long-term, whole-ecosystem studies of the response of biodiversity to high O₃, particularly in the temperate zone.
 - To what extent are the toxic effects of high O₃ on biodiversity mediated by simultaneous exposure to high CO₂?
 - What are the direct effects of high O₃ on higher trophic levels?
5. Investigate ultra-violet radiation, including the effects of high UV-B flux on biodiversity, particularly in high arctic terrestrial and marine ecosystems.
 - Are global increases in UV-B flux leading to a loss of amphibian biodiversity?
 - Are high-latitude increases in UV-B flux altering the structure and function of arctic ecosystems?

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LITERATURE CITED

- Ackerly, D.D., and F.A. Bazzaz. 1995. Plant growth and reproduction along CO₂ gradients: Non-linear responses and implications for community change. *Global Change Biology* 1: 199–207.
- Ahas, R. 1999. Long-term phyto-, ornitho-, and ichthyophenological time-series analyses in Estonia. *International Journal of Biometeorology* 42: 119–123.
- Alford, R.A., and S.J. Richards. 1999. Global amphibian declines: A problem in applied ecology. *Annual Review of Ecology and Systematics* 30: 133–165.
- Allen, C.D., and D. D. Breshears. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences USA* 95: 14839–14841.
- Andalo, C., C. Raquin, N. Machon, B. Godelle, and M. Mousseau. 1998. Direct and maternal effects of elevated CO₂ on early root growth of germinating *Arabidopsis thaliana* seedlings. *Annals of Botany* 81: 405–411.
- Andrews, J.A., R. Matamala, K.M. Westover, and W.H. Schlesinger. 2000. Temperature effects on the diversity of soil heterotrophs and the $\delta^{13}\text{C}$ of soil-respired CO₂. *Soil Biology and Biochemistry* 32: 699–706.
- Arft, A.M., and the ITEX Group. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69: 491–511.
- Arnold, J.A., and J.C. Gordon. 1990. Effect of nodulation, nitrogen fixation and CO₂ enrichment on the physiology, growth and dry mass allocation of seedlings of *Alnus rubra* Bong. *New Phytologist* 116: 55–66.
- Aronson, R.B., W.F. Precht, I.G. Macintyre, and T.J.T. Murdoch. 2000. Coral bleach-out in Belize. *Nature* 405: 36.
- Arris, L.L., and P.S. Eagleson. 1989. Evidence of a physiological basis for the boreal-deciduous ecotone in North America. *Vegetatio* 82: 55–58.
- Ashmore, M.R., and N. Ainsworth. 1995. The effects of cutting on the species composition of artificial grassland communities. *Functional Ecology* 9: 708–712.
- Ashmore, M.R., R.H. Thwaites, N. Ainsworth, D.S. Cousins, S.A. Power, and A.J. Morton. 1995. Effects of ozone on calcareous grassland communities. *Water, Air, and Soil Pollution* 85: 1527–1532.
- Austin, M.P., and B.O. Austin. 1980. Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology* 68: 891–918.
- Bakelaar, R.G., and E.P. Odum. 1978. Community and population level responses to fertilization in an old-field ecosystem. *Ecology* 59: 660–665.
- Barbo, D.N., A.H. Chappelka, G.L. Somers, M.S. Miller-Goodman, and K. Stolte. 1998. Diversity of an early successional plant community as influenced by ozone. *New Phytologist* 138: 653–662.

- Barnes, J., J. Bender, T. Lyons, and A. Borland. 1999. Natural and man-made selection for air pollution resistance. *Journal of Experimental Botany* 50: 1423–1435.
- Barnola, J. M., D. Raynaud, Y. S. Korotevich, and C. Lorius. 1987. Vostok ice core provides 160,000 year record of atmospheric CO₂. *Nature* 329:408–414.
- Barry, J.P., C.H. Baxter, R.D. Sagarin, and S.E. Gilman. 1995. Climate-related long-term faunal changes in a California rocky intertidal community. *Science* 267: 672–675.
- Barton, A.M., and J.A. Terri. 1993. The ecology of elevational positions in plants: Drought resistance in five montane pine species in southeastern Arizona. *American Journal of Botany* 80: 15–25.
- Bazzaz, F.A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology* 56: 485–488.
- Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global CO₂ levels. *Annual Review of Ecology and Systematics* 21: 167–196.
- Bazzaz, F.A. 1996. *Plants in Changing Environments*. New York: Cambridge University Press.
- Bazzaz, F.A., J.S. Coleman, and S.R. Morse. 1990. Growth responses of seven major co-occurring tree species of the northeastern United States to elevated CO₂. *Canadian Journal of Forest Research* 20: 1479–1489.
- Bazzaz, F.A., and S.L. Miao. 1993. Successional status, seed size, and responses of tree seedlings to CO₂, light and nutrients. *Ecology* 74: 104–112.
- Bazzaz, F.A., and S.T.A. Pickett. 1980. Physiological ecology of tropical succession: A comparative review. *Annual Review of Ecology and Systematics* 11: 287–310.
- Behrenfeld, M.J., J.T. Hardy, H. Gucinski, A. Hanneman, H. Lee, and A. Wones. 1993. Effects of ultraviolet-B radiation on primary production along latitudinal transects in the south Pacific ocean. *Marine Environmental Research* 35: 349–363.
- Bell, K.L., and L.C. Bliss. 1979. Autecology of *Kobresia bellardii*: Why winter snow accumulation limits local distribution. *Ecological Monographs* 49: 377–402.
- Bennett, J.P., P. Rassat, P. Berrang, and D.F. Karnosky. 1992. Relationship between leaf anatomy and ozone sensitivity of *Fraxinus pennsylvanica* Marsh. and *Prunus serotina* Ehrh. *Environmental and Experimental Botany* 32: 33–41.
- Bennett, J.P., and V.C. Runeckles. 1977. Effects of low levels of ozone on plant competition. *Journal of Applied Ecology* 14: 877–880.
- Berrang, P., D.F. Karnosky, and J.P. Bennett. 1989. Natural selection for ozone tolerance in *Populus tremuloides*: Field verification. *Canadian Journal of Forest Research* 19: 519–522.
- Bethke, R.W., and T.D. Nudds. 1995. Effects of climate change and land use on duck abundance in Canadian prairie-parklands. *Ecological Applications* 5: 588–601.
- Bezemer, T.M., and T.H. Jones. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂: Quantitative analyses and guild effects. *Oikos* 82: 212–222.
- Blake, L., K.W.T. Goulding, C.J.B. Mott, and A.E. Johnson. 1999. Changes in soil chemistry accompanying acidification over more than 100 years under woodland and grass at Rothamsted Experiment Station, UK. *European Journal of Soil Science* 50: 401–412.

- Blaustein, A.R., P.D. Hoffman, D.G. Hokit, J.M. Kiesecker, S.D. Wallis, and J.B. Hayes. 1994. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines? *Proceedings of the National Academy of Sciences USA* 91: 1791–1795.
- Bobbink, R. 1991. Effects of nutrient enrichment in Dutch chalk grassland. *Journal of Applied Ecology* 28: 28–41.
- Bothwell, M.L., D.M.J. Sherbot, and D.M. Pollock. 1994. Ecosystem response to solar ultraviolet-B radiation: Influence of trophic-level interactions. *Science* 265: 97–100.
- Broecker, W. S. 1997. Thermohaline circulation, the Achilles heel of our climate system: Will man-made CO₂ upset the current balance? *Science* 278:1582–1588.
- Brown, B. 1997. Coral bleaching: Causes and consequences. *Coral Reefs* 16 (Suppl.): 129–138.
- Brown, J.H. 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. *American Naturalist* 105: 467–478.
- Brown, J.H., T.J. Valone, and C.G. Curtin. 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences USA* 94: 9729–9733.
- Brown, K.R., and K.O. Higginbotham. 1986. Effects of carbon dioxide enrichment and nitrogen supply on growth of boreal tree seedlings. *Tree Physiology* 2: 223–232.
- Bruce, K.D., T.H. Jones, T.M. Bezemer, L.J. Thompson, and D.A. Ritchie. 2000. The effect of elevated atmospheric carbon dioxide levels on soil bacterial communities. *Global Change Biology* 6: 427–434.
- Bungener, P., G.R. Balls, S. Nussbaum, M. Geissmann, A. Grub, and J. Fuhrer. 1999. Leaf injury characteristics of grassland species exposed to ozone in relation to soil moisture condition and vapour pressure deficit. *New Phytologist* 142: 271–282.
- Bungener, P., S. Nussbaum, A. Grub, and J. Fuhrer. 1999. Growth response of grassland species to ozone in relation to soil moisture and plant strategy. *New Phytologist* 142: 283–293.
- Cain, M.L., H. Damman, and A. Muir. 1998. Holocene migration of woodland herbs. *Ecological Monographs* 68: 325–347.
- Caldwell, M.M., and S.D. Flint. 1994. Stratospheric ozone reduction, solar UV-B radiation and terrestrial ecosystems. *Climatic Change* 28: 375–394.
- Cerling, T.E., J.M. Harris, B.J. MacFadden, M.G. Leakey, J. Quade, V. Elsenmann, and J.R. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389: 153–158.
- Cerling, T., Y. Wang, and J. Quade. 1993. Expansion of C4 ecosystems as an indicator of global ecological change in the Late Miocene. *Nature* 361: 344–345.
- Chameides, W.L., P.S. Kasibhatla, J. Yienger, and H. Levy. 1994. Growth of continental-scale metro-agro-plexes, regional ozone pollution, and world food production. *Science* 264: 74–77.
- Chapin, F.S., G.R. Shaver, A.E. Giblin, K.J. Nadelhoffer, and J.A. Laundre. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694–711.

- Chappelka, A., J. Renfro, G. Somers, and B. Nash. 1997. Evaluation of ozone injury on foliage of black cherry (*Prunus serotina*) and tall milkweed (*Asclepias exaltata*) in Great Smoky Mountains National Park. *Environmental Pollution* 95: 13–18.
- Chappelka, A.H., and L.J. Samuelson. 1998. Ambient ozone effects on forest trees of the eastern United States: A review. *New Phytologist* 139: 91–108.
- Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleo record. *American Naturalist* 152:204–224.
- Clark, J. S., C. Fastie, G. Hurtt, S. T. Jackson, C. Johnson, G. King, M. Lewis, J. Lynch, S. Pacala, I.C. Prentice, E. W. Schupp, T. Webb III, and P. Wyckoff. 1998. Reid's Paradox of rapid plant migration. *BioScience* 48:13–24.
- Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: Variation in dispersal and reproduction retards population spread. *American Naturalist* 157: 537–554.
- Clark, J.S., E.C. Grimm, J. Lynch, and P.J. Mueller. 2001. Effects of climate change on the C4 grassland/woodland boundary in the northern Central Plains. *Ecology* 82: 620–636.
- Clark, J.S., B. Beckage, J. HilleRisLambers, I. Ibanez, S. LaDeau, J. MacLachlan, J. Mohan, and M. Rocca. 2001. Dispersal and plant migration. In H. Mooney and J. Canadell (eds.), *Encyclopedia of Global Environmental Change*, Volume 8. London: John Wiley and Sons.
- Clark, P. U., R. B. Alley, and D. Pollard. 1999. Northern Hemisphere ice-sheet influences on global climate change. *Science* 286:1104–1111.
- COHMAP. 1988. Climatic changes of the last 18,000 years: Observations and model simulations. *Science* 241:1043–1052.
- Cole, D.R., and H.C. Monger. 1994. Influence of atmospheric CO₂ on the decline of C4 plants during the last deglaciation. *Nature* 368: 533–536.
- Collatz, G. J., J.A. Berry, and J.S. Clark. 1998. Effects of climate and atmospheric CO₂ partial pressure on the global distribution of C4 grasses: Present, past, and future. *Oecologia* 114:441–454.
- Comes, H. P., and J. W. Kadereit. 1998. The effect of Quaternary climatic changes on plant distribution and evolution. *Trends in Plant Science Reviews* 3:432–438.
- Coope, G.R. 1987. The response of late Quaternary insect communities to sudden climatic changes. In J.H.R. Gee and P.S. Giller (eds.). *Organization of Communities—Past and Present*, pp. 421–438. Oxford: Blackwell.
- Cooper, S.L., and D.L. Peterson. 2000. Spatial distribution of tropospheric ozone in western Washington, USA. *Environmental Pollution* 107: 339–347.
- Correll, D.L., C.O. Clark, B. Goldberg, V.R. Goodrich, D.R. Hayes, W.H. Klein, and W.D. Schecher. 1992. Spectral ultraviolet-B radiation fluxes at the earth's surface: Long-term variations at 39°N, 77°W. *Journal of Geophysical Research* 97: 7579–7591.
- Cummins, C.P., P.D. Greenslade, and A.R. McLeod. 1999. A test of the effect of supplemental UV-B radiation on the common frog, *Rana temporaria* L., during embryonic development. *Global Change Biology* 5: 471–479.
- Curtis, P.S., D.J. Klus, S. Kalisz, and S.J. Tonsor. 1996. Intraspecific variation in CO₂ response in *Raphanus raphanistrum* and *Plantago lanceolata*: Assessing the poten-

- tial for evolutionary change with rising atmospheric CO₂. In C. Korner and F. Bazzaz (eds.), *Carbon Dioxide, Populations and Communities*, pp. 13–22. San Diego: Academic Press.
- Curtis, P.S., and X. Wang. 1998. A meta-analysis of elevated CO₂ effects on woody plant mass, form, and physiology. *Oecologia* 113: 299–313.
- Cybulski, W.J., and W.T. Peterjohn. 1999. Effects of ambient UV-B radiation on the above-ground biomass of seven temperate-zone plant species. *Plant Ecology* 145: 175–181.
- Davidson, E.A., C.S. Potter, P. Schlesinger, and S.A. Klooster. 1998. Model estimates of regional nitric oxide emissions from soils of the southeastern United States. *Ecological Applications* 8: 748–759.
- Davis, M. B. 1981. Quaternary history and the stability of forest communities. In D.C. West, H. H. Shugart, D.B. Botkin (eds.), *Forest Succession: Concepts and Application*, pp. 132–153. New York: Springer-Verlag.
- Davis, M. B., and C. Zabinski. 1992. Changes in geographical range resulting from greenhouse warming: Effects on biodiversity in forests. In R. Peters and T. Lovejoy (eds.), *Global Warming and Biological Diversity*, pp. 297–308. New Haven, Conn.: Yale University Press.
- Davison, A.W., and J.D. Barnes. 1998. Effects of ozone on wild plants. *New Phytologist* 139: 135–151.
- Day, T.A., C.T. Ruhland, C.W. Grobe, and F. Xiong. 1999. Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. *Oecologia* 119: 24–35.
- Day, T.A., T.C. Vogelmann, and E.H. DeLucia. 1992. Are some plant life forms more effective than others in screening out ultraviolet-B radiation? *Oecologia* 92: 513–519.
- Degens, B.P., L.A. Schipper, G.P. Sparling, M. Vojvodic-Vukovic. 2000. Decreases in organic C reserves in soils can reduce the catabolic diversity of soil microbial communities. *Soil Biology and Biochemistry* 32: 189–196.
- Delcourt, P.A., and H.R. Delcourt. 1987. *Long-Term Forest Dynamics of the Temperate Zone*. New York: Springer-Verlag.
- DeLucia, E.H., R.M. Callaway, E.M. Thomas, and W.H. Schlesinger. 1997. Mechanisms of phosphorus acquisition for ponderosa pine seedlings under high CO₂ and temperature. *Annals of Botany* 79: 111–120.
- DeLucia, E.H., J.G. Hamilton, S.L. Naidu, R.B. Thomas, J.A. Andrews, A. Finzi, M. Lavine, R. Matamala, J.E. Mohan, G.R. Hendrey, and W.H. Schlesinger. 1999. Net primary production of a forest ecosystem with experimental CO₂ enrichment. *Science* 284: 1177–1179.
- DeLucia, E.H., and W.H. Schlesinger. 1990. Ecophysiology of Great Basin and Sierra Nevada vegetation on contrasting soils. In C.B. Osmond, L.F. Pitelka, and G.M. Hidy (eds.), *Plant Biology of the Basin and Range*, pp. 143–178. New York: Springer-Verlag.
- Demesure, B., B. Comps, and R. J. Petit. 1996. Chloroplast DNA phylogeography of the common beech (*Fagus sylvatica* L.) in Europe. *Evolution* 50:2515–2520.

- Dillenburg, L. R., A. H. Teramura, I. N. Forseth, and D. F. Whigham. 1995. Photosynthetic and biomass allocation responses of *Liquidambar styraciflua* (Hamamelidaceae) to vine competition. *American Journal of Botany* 82(4): 454–461.
- Dippery, J.K., D.T. Tissue, R.B. Thomas, and B.R. Strain. 1995. Effects of low and elevated CO₂ on C3 and C4 annuals. I. Growth and biomass allocation. *Oecologia* 101: 13–20.
- Docherty, M., D.K. Hurst, J.K. Holopainen, J.B. Whittaker, P.J. Lee, and A.D. Watt. 1996. Carbon dioxide-induced changes in beech foliage cause female beech weevil larvae to feed in a compensatory manner. *Global Change Biology* 2: 335–342.
- Dumolin-Lapeque, S., B. Demesure, S. Fineschi, V. Le Corre, and R. J. Petit. 1997. Phylogeographic structure of white oaks throughout the European continent. *Genetics* 146:1475–1487.
- Dunn, P.O., and D.W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London* 266B: 2487–2490.
- Evans, L.S., K. Albury, and N. Jennings. 1996. Relationships between anatomical characteristics and ozone sensitivity of leaves of several herbaceous dicotyledonous plant species at Great Smoky Mountains National Park. *Environmental and Experimental Botany* 36: 413–420.
- Evans, L.S., and P.R. Miller. 1972. Comparative needle anatomy and relative ozone sensitivity of four pine species. *Canadian Journal of Botany* 50: 1067–1071.
- Fairbanks, R. G. 1989. A 17,000-year glacio-eustatic sea level record: Influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature* 342:637–642.
- Farnsworth, E.J., J. Nunez-Farfan, S.A. Careaga, and F.A. Bazzaz. 1995. Phenology and growth of three temperate forest life forms in response to soil warming. *Journal of Ecology* 83: 967–977.
- Fiscus, E.L., J.E. Miller, F.L. Booker, A.S. Heagle, and C.D. Reid. 2001. The impact of ozone and other limitations on crop productivity response to CO₂. *Technology*, in press.
- Fiscus, E.L., C.D. Reid, J.E. Miller, and A.S. Heagle. 1997. Elevated CO₂ reduces O₃ flux and O₃-induced yield losses in soybeans: Possible implications for elevated CO₂ studies. *Journal of Experimental Botany* 48: 307–313.
- Fishman, J., C.E. Watson, J.C. Larsen, and J.A. Logan. 1990. Distribution of tropospheric ozone determined from satellite data. *Journal of Geophysical Research* 95: 3599–3617.
- Foley, J. A., J. E. Kutzbach, M. T. Coe, and S. Levis. 1994. Feedbacks between climate and boreal forests during the Holocene epoch. *Nature* 371:52–54.
- Fowler, D., C. Flechard, U. Skiba, M. Coyle, and J.N. Cape. 1998. The atmospheric budget of oxidized nitrogen and its role in ozone formation and deposition. *New Phytologist* 139: 11–23.
- Freedman, B., and T.C. Hutchinson. 1980. Long-term effects of smelter pollution at Sudbury, Ontario, on forest community composition. *Canadian Journal of Botany* 58: 2123–2140.

- Fuhrer, J., H. Shariat-Madari, R. Perler, W. Tschannen, and A. Grub. 1994. Effects of ozone on managed pasture. II. Yield, species composition, canopy structure, and forage quality. *Environmental Pollution* 86: 307–314.
- Fuhrer, J., L. Skarby, and M.R. Ashmore. 1997. Critical levels for ozone effects on vegetation in Europe. *Environmental Pollution* 97: 91–106.
- Galen, C., and M.L. Stanton. 1993. Short-term responses of alpine buttercups to experimental manipulations of growing season length. *Ecology* 74: 1052–1058.
- Galen, C., and M.L. Stanton. 1995. Response of snowbed plant species to changes in growing-season length. *Ecology* 76: 1546–1557.
- George, T.L., A.C. Fowler, R.L. Knight, and L.C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. *Ecological Applications* 2: 275–284.
- Glynn, P.W. 1996. Coral reef bleaching: Facts, hypotheses, and implications. *Global Change Biology* 2: 495–509.
- Godbold, D.L., G.M. Berntson, and F.A. Bazzaz. 1997. Growth and mycorrhizal colonization of three North American tree species under elevated atmospheric CO₂. *New Phytologist* 137: 433–440.
- Gold, W.G., and M.M. Caldwell. 1983. The effects of ultraviolet-B radiation on plant competition in terrestrial ecosystems. *Physiologia Plantarum* 58: 435–444.
- Graham, R. W., and E. C. Grimm. 1990. Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology and Evolution* 5: 289–292.
- Grams, T.E.E., S. Anegg, K.-H. Haberle, C. Langebartels, and R. Matyssek. 1999. Interactions of chronic ozone exposure to elevated CO₂ and O₃ levels in the photosynthetic light and dark reactions of European beech (*Fagus sylvatica*). *New Phytologist* 144: 95–107.
- Graveland, J., R. van der Wal, J.H. van Balen, and A.J. van Noordwijk. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature* 368: 446–448.
- Grime, J.P., V.K. Brown, K. Thompson, G.J. Masters, S.H. Hillier, I.P. Clarke, A.P. Askew, D. Corker, and J.P. Kiely. 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* 289: 762–765.
- Harte, J., A. Rawa, and V. Price. 1996. Effects of manipulated soil microclimate on mesofaunal biomass and diversity. *Soil Biology and Biochemistry* 28: 313–322.
- Harte, J., and R. Shaw. 1995. Shifting dominance within a montane vegetation community: Results of a climate-warming experiment. *Science* 267: 876–880.
- Harte, J., M.S. Torn, F.-R. Chang, B. Feifarek, A.P. Kinzig, R. Shaw, and K. Shen. 1995. Global warming and soil microclimate: Results from a meadow-warming experiment. *Ecological Applications* 5: 132–150.
- Hattenschwiler, S., and C. Korner. 1996. Effects of elevated CO₂ and increased nitrogen deposition on photosynthesis and growth of understory plants in spruce model ecosystems. *Oecologia* 106: 172–180.
- Hattenschwiler, S., and C. Korner. 2000. Tree seedling responses to *in situ* CO₂ enrichment differ among species and depend on understorey light availability. *Global Change Biology* 6: 213–226.

- Hattenschwiler, S., F. Miglietta, A. Raschi, and C. Korner. 1997. Thirty years of *in situ* tree growth under elevated CO₂: A model for future forest responses? *Global Change Biology* 3: 463–471.
- Heagle, A.S. 1989. Ozone and crop yield. *Annual Review of Phytopathology* 27: 397–423.
- Heagle, A.S., R.L. Brandenburg, J.C. Burns, and J.E. Miller. 1994. Ozone and carbon dioxide effects on spider mites in white clover and peanut. *Journal of Environmental Quality* 23: 1168–1176.
- Heath, R.L. 1994. Alterations of plant metabolism by ozone exposure. In R.G. Alscher and A.R. Wellburn (eds.), *Plant Responses to the Gaseous Environment*, pp. 121–145. London: Chapman and Hall.
- Heil, G.W., and W.H. Diemont. 1983. Raised nutrient levels change heathland into grassland. *Vegetatio* 53: 113–120.
- Hein, M., and K. Sand-Jensen. 1997. CO₂ increases oceanic primary production. *Nature* 388: 526–527.
- Heller, H.C., and D.M. Gates. 1971. Altitudinal zonation of chipmunks (*Eutamias*): Energy budgets. *Ecology* 52: 424–433.
- Hewitt, G. M. 1990. Divergence and speciation as viewed from an insect hybrid zone. *Canadian Journal of Zoology* 68: 1701–1715.
- Hewitt, G. M. 1999. Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68: 87–112.
- Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* 405: 907–913.
- Hirose, T., D.D. Ackerly, M.B. Traw, and F.A. Bazzaz. 1996. Effects of CO₂ elevation on canopy development in the stands of two co-occurring annuals. *Oecologia* 108: 215–223.
- Hodge, A., E. Paterson, S.J. Grayston, C.D. Campbell, B.G. Ord, and K. Killham. 1998. Characterization and microbial utilisation of exudate material from the rhizosphere of *Lolium perenne* grown under CO₂ enrichment. *Soil Biology and Biochemistry* 30: 1033–1043.
- Hoffman, R.W., E.E. Swinney, S.J. Bloor, K. R. Markam, K.G. Ryan, B.D. Campbell, B.R. Jordan, and D.W. Fountain. 2000. Responses of nine *Trifolium repens* L. populations to ultraviolet-B radiation: Differential flavonol glycoside accumulation and biomass production. *Annals of Botany* 86: 527–537.
- Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. *Canadian Journal of Forest Research* 24: 1835–1845.
- Holland, E.A., B.H. Braswell, J.-F. Lamarque, A. Townsend, J. Sulzman, J.-F. Muller, F. Dentener, G. Brasseur, H. Levy, J.E. Penner, and G.-J. Roelofs. 1997. Variations in the predicted spatial distribution of atmospheric nitrogen deposition and their impact on carbon uptake by terrestrial ecosystems. *Journal of Geophysical Research* 102: 15849–15866.
- Hopkins, M. S., A. W. Graham, R. Hewett, J. Ash, and J. Head. 1990. Evidence of late Pleistocene fires and eucalypt forest from a North-Queensland humid tropical rainforest site. *Australian Journal of Ecology* 15:345–347.
- Hudson, J.W., and D.B. Deavers. 1973. Metabolism, pulmocutaneous water loss and respiration of eight species of ground squirrels from different environments. *Comparative Biochemistry and Physiology* 45(1A): 69–100.

- Huenneke, L.F., S.P. Hamburg, R. Koide, H.A. Mooney, and P.M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in California serpentine grassland. *Ecology* 71: 478–491.
- Hunter, J.R., S.E. Kaupp, and J.H. Taylor. 1981. Effects of solar and artificial ultraviolet-B radiation on larval northern anchovy, *Engraulis mordax*. *Photochemistry and Photobiology* 34: 477–486.
- Huntley, B., and H.J.B. Birks. 1983. *An Atlas of Past and Present Pollen Maps for Europe 0–13,000 Years Ago*. Cambridge, Mass.: Cambridge University Press.
- Hurd, L.E., M.V. Mellinger, L.L. Wolf, and S.J. McNaughton. 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. *Science* 173: 1134–1136.
- Hurrell, J.W., and K.E. Trenbert. 1997. Spurious trends in satellite MSU temperatures from merging different satellite records. *Nature* 386: 164–167.
- Ibrahim, K. M., R. A. Nichols, and G. M. Hewitt. 1996. Spatial patterns of genetic variation generated by different forms of dispersal during range expansion. *Heredity* 77:282–291.
- Idso, S.B. 1999. The long-term response of trees to atmospheric CO₂ enrichment. *Global Change Biology* 5: 493–495.
- Islam, K.R., C.L. Mulchi, and A.A. Ali. 2000. Interactions of tropospheric CO₂ and O₃ enrichments and moisture variations on microbial biomass and respiration in soil. *Global Change Biology* 6: 255–265.
- Iverson, L.R., and A.M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs* 68: 465–485.
- Jackson, S. T., and C. Weng. 1999. Late Quaternary extinction of a tree species in eastern North America. *Proceedings of the National Academy of Sciences* 96: 13847–13852.
- Jiang, Y., and Y.L. Yung. 1996. Concentrations of tropospheric ozone from 1979 to 1992 over the tropical Pacific South America from TOMS data. *Science* 272: 714–716.
- Jobbagy, E.G., and R.B. Jackson. 2000. Global controls of forest line elevation in the northern and southern hemispheres. *Global Ecology and Biogeography* 9: 253–268.
- Johannessen, O.M., E.V. Shalina, and M.W. Miles. 1999. Satellite evidence for an arctic sea ice cover in transformation. *Science* 286: 1937–1939.
- Johnson, H.B., H.W. Polley, and H.S. Mayeux. 1993. Increasing CO₂ and plant-plant interactions: Effects of natural vegetation. *Vegetatio* 104/105: 157–170.
- Johnston, K.M., and O.J. Schmitz. 1997. Wildlife and climate change: Assessing the sensitivity of selected species to simulated doubling of atmospheric CO₂. *Global Change Biology* 3: 531–544.
- Jones, C.G., J.S. Coleman, and S. Findlay. 1994. Effects of ozone on interactions between plants, consumers and decomposers. In R.G. Alscher and A.R. Wellburn (eds.), *Plant Responses to the Gaseous Environment*, pp. 339–364. London: Chapman and Hall.
- Jones, T.H., L.J. Thompson, J.H. Lawton, T.M. Bezemer, R.D. Bardgett, T.M. Blackburn, K.D. Bruce, P.F. Cannon, G.S. Hall, S.E. Hartley, G. Howson, C.G. Jones, C. Kampichler, E. Kandeler, and D.A. Ritchie. 1998. Impacts of ris-

- ing atmospheric carbon dioxide on model terrestrial ecosystems. *Science* 280: 441–443.
- Justic, D., N.N. Rabalais, R.E. Turner, and Q. Dortch. 1995. Changes in nutrient structure of river-dominated coastal waters: Stoichiometric nutrient balance and its consequences. *Estuarine, Coastal and Shelf Science* 40: 339–356.
- Kellomäki, S., and K.-Y. Wang. 1997a. Effects of elevated O_3 and CO_2 on chlorophyll fluorescence and gas exchange in Scots pine during the third growing season. *Environmental Pollution* 97: 17–27.
- Kellomäki, S., and K.-Y. Wang. 1997b. Effects of elevated O_3 and CO_2 concentrations on photosynthesis and stomatal conductance in Scots pine. *Plant, Cell and Environment* 29: 995–1006.
- Kempton, R.A. 1979. The structure of species diversity and measurement of diversity. *Biometrics* 35: 307–321.
- Kerr, J.B., and C.T. McElroy. 1993. Evidence for large upward trends of ultraviolet B radiation linked to ozone depletion. *Science* 262: 1032–1034.
- Kershaw, A. P. 1993. The development of rainforest-savanna boundaries in tropical Australia. In P.A. Farley, J. Proctor, and J.A. Ratter (eds.), *Nature and Dynamics of Forest Savanna Boundaries*, pp. 255–271. London: Chapman and Hall.
- Kerstiens, G. 1998. Shade-tolerance as a predictor of responses to elevated CO_2 in trees. *Physiologia Plantarum* 102:472–480.
- Kleypas, J.A., R.W. Buddemeir, D. Archer, J.-P. Gattuso, C. Langdon, and B.N. Opdyke. 1999. Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science* 284: 118–120.
- Klironomos, J.N., and M.F. Allen. 1995. UV-B-mediated changes on below-ground communities associated with the roots of *Acer saccharum*. *Functional Ecology* 9:923–930.
- Klironomos, J.N., M.C. Rillig, and M.F. Allen. 1996. Below-ground microbial and microfaunal responses to *Artemisia tridentata* grown under elevated atmospheric CO_2 . *Functional Ecology* 10: 527–534.
- Klironomos, J.N., M.G. Rillig, M.F. Allen, D.R. Zak, M. Kubiskes, and K.S. Pregitzer. 1997. Soil fungal-arthropod responses to *Populus tremuloides* grown under enriched atmospheric CO_2 under field conditions. *Global Change Biology* 3: 473–478.
- Klironomos, J.N., M. Ursic, M. Rillig, and M.F. Allen. 1998. Interspecific differences in the response of arbuscular mycorrhizal fungi to *Artemisia tridentata* grown under elevated atmospheric CO_2 . *New Phytologist* 138: 599–605.
- Kubiske, M.E., and K.S. Pregitzer. 1996. Effects of elevated CO_2 and light availability on the photosynthetic light response of trees of contrasting shade tolerance. *Tree Physiology* 16: 351–358.
- Kullman, L. 1996. Norway spruce present in the Scandes Mountains, Sweden at 8000 yr BP: New light on Holocene tree spread. *Global Ecology and Biogeography Letters* 5: 94–101.
- Kutzbach, J. E., and P. J. Guetter. 1986. The influence of changing orbital parameters and surface boundary conditions on climate simulations for the past 18000 years. *Journal of Atmospheric Sciences* 43: 1726–1759.
- Kutzbach, J. E., P. J. Guetter, P. J. Behling, and R. Selin. 1993. Simulated climatic

- changes: Results of the COHMAP climate-model experiments. In H.E. Wright Jr., J. E. Kutzbach, T. Webb III, W.F. Ruddiman, F.A. Street-Perrott, and P.J. Bartlein (eds.), *Global Climates since the Last Glacial Maximum*, pp. 24–93. Minneapolis: University of Minnesota Press.
- Laakso, K., and S. Huttunen. 1998. Effects of ultraviolet-B radiation (UV-B) on conifers: A review. *Environmental Pollution* 99: 319–328.
- Lawrence, M.G., and P.J. Crutzen. 1999. Influence of NO_x emissions from ships on tropospheric photochemistry and climate. *Nature* 402: 167–170.
- Leadley, P.W., P.A. Niklaus, R. Stocker, and C. Korner. 1999. A field study of the effects of elevated CO₂ on plant biomass and community structure in a calcareous grassland. *Oecologia* 118: 39–49.
- Leclercq, N., J.-P. Gattuso, and J. Jaubert. 2000. CO₂ partial pressure controls the calcification rate of a coral community. *Global Change Biology* 6: 329–334.
- LeCorre, A., N. Machon, R. J. Petit, and A. Kremer. 1997. Colonization with long-distance seed dispersal and genetic structure of maternally inherited genes in forest trees: A simulation study. *Genetic Research* 69: 117–125.
- Levin, S.A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* 104: 413–423.
- Levy, H., P.S. Kasibhatla, W.J. Moxim, A.A. Klonecki, A.I. Hirsch, S.J. Oltmans, and W.L. Chameides. 1997. The global impact of human activity on tropospheric ozone. *Geophysical Research Letters* 14: 791–794.
- Lindroth, R.L., K.K. Kinney, and C.L. Platz. 1993. Responses of deciduous trees to elevated atmospheric CO₂: Productivity, phytochemistry, and insect performance. *Ecology* 74: 763–777.
- Lindroth, R.L., P.B. Reich, M.G. Tjoelker, J.C. Volin, and J. Oleksyn. 1993. Light environment alters response to ozone stress in seedlings of *Acer saccharum* Marsh. and hybrid *Populus* L. 3. Consequences for performance of gypsy moth. *New Phytologist* 124: 647–651.
- Lukeville, A., and R.F. Wright. 1997. Experimentally increased soil temperature causes release of nitrogen at a boreal forest catchment in southern Norway. *Global Change Biology* 3: 13–22.
- Luscher, A., T. Hebeisen, S. Zanetti, U.A. Hartwig, H. Blum, G.R. Hendrey, and J. Nosberger. 1996. Differences between legumes and nonlegumes of permanent grassland in their responses to Free-Air Carbon Dioxide Enrichment: Its effect on competition in a multispecies mixture. In C. Korner and F.A. Bazzaz (eds.), *Carbon Dioxide, Populations, and Communities*, pp. 287–300. San Diego: Academic Press.
- Lyons, T.M., J.D. Barnes, and A.W. Davison. 1997. Relationships between ozone resistance and climate in European populations of *Plantago major*. *New Phytologist* 136: 503–510.
- MacPhee, R.D.E. 1999. *Extinctions in Near Time*. New York: Kluwer Academic.
- MaGill, A.H., J.D. Aber, J.J. Hendricks, R.D. Bowden, J.M. Melillo, and P.A. Steudler. 1997. Biogeochemical response of forest ecosystems to simulated nitrogen deposition. *Ecological Applications* 7: 402–415.
- Martin, P. S., and R. G. Klein. 1984. *Quaternary Extinctions*. Tucson: University of Arizona Press.

- Mayewski, P.A., and M.R. Legrand. 1990. Recent increase in nitrate concentration of Antarctic snow. *Nature* 346: 258–260.
- Mayewski, P.A., W.B. Lyons, M.J. Spencer, M. Twickler, W. Dansgaard, B. Koci, C.I. Davidson, and R.E. Honrath. 1986. Sulfate and nitrate concentrations from a south Greenland ice core. *Science* 232: 975–977.
- McAndrews, J.H. 1966. Postglacial history of prairie, savanna, and forest in northwestern Minnesota. *Memoirs of the Torrey Botanical Club* 22: 1–72.
- McCauley, E., and W.W. Murdoch. 1990. Predator-prey dynamics in rich and poor environments. *Nature* 343: 455–457.
- McClenahan, J.R. 1978. Community changes in a deciduous forest exposed to air pollution. *Canadian Journal of Forest Research* 8: 432–438.
- McKee, I.F., J.F. Bullimore, and S.P. Long. 1997. Will elevated CO₂ concentrations protect the yield of wheat from O₃ damage? *Plant, Cell and Environment* 20: 77–84.
- McKee, I.F., P.K. Farage, and S.P. Long. 1995. The interactive effects of elevated CO₂ and O₃ concentration on photosynthesis in spring wheat. *Photosynthesis Research* 45: 111–119.
- McKenzie, R., B. Connor, and G. Bodeker. 1999. Increased summertime UV radiation in New Zealand in response to ozone loss. *Science* 285: 1709–1711.
- McMinn, A., H. Heijnis, and D. Hodgson. 1994. Minimal effects of UVB radiation on Antarctic diatoms over the past 20 years. *Nature* 370: 547–549.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* 285: 1396–1398.
- Miller, J.E. 1988. Effects of photosynthesis, carbon allocation, and plant growth associated with air pollutant stress. In W.W. Heck, O.C. Taylor, and D.T. Tingey (eds.), *Assessment of Crop Loss from Air Pollutants*, pp. 287–314. London: Elsevier Science.
- Miller, J.E., A.S. Heagle, and W.A. Pursley. 1998. Influence of ozone stress on soybean response to carbon dioxide enrichment. II. Biomass and Development. *Crop Science* 38: 122–128.
- Mitchell, J.F.B., S. Manabe, V. Meleshko, and T. Ookioka. 1990. Equilibrium climate change—and its implications for the future. In J.T. Houghton, G.J. Jenkins, and J.J. Ephraums (eds.), *Climate Change: The IPCC Scientific Assessment*, pp. 131–164. Cambridge: Cambridge University Press.
- Montealegre, C.M., C. van Kessel, J.M. Blumenthal, H-G. Hur, U.A. Hartwig, and M.J. Sadowsky. 2000. Elevated atmospheric CO₂ alters microbial population structure in a pasture ecosystem. *Global Change Biology* 6: 475–482.
- Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1997. Effects of elevated carbon dioxide and ozone on the growth and yield of spring wheat (*Triticum aestivum* L.). *Journal of Experimental Botany* 48: 113–122.
- Mulholland, B.J., J. Craigon, C.R. Black, J.J. Colls, J. Atherton, and G. Landon. 1998. Growth, light interception and yield responses of spring wheat (*Triticum aestivum* L.) grown under elevated atmospheric CO₂ and O₃ in open-top chambers. *Global Change Biology* 4: 121–130.
- Mun, H.T., and W.G. Whitford. 1989. Effects of nitrogen amendment on annual plants in the Chihuahuan Desert. *Plant and Soil* 120: 225–231.

- Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar, and R.R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698–702.
- Naeem, S., D.R. Hahn, and G. Schuurman. 2000. Producer-decomposer co-dependency influences biodiversity effects. *Nature* 403: 762–764.
- Nash, T.H. 1975. Influence of effluents from a zinc factory on lichens. *Ecological Monographs* 45: 183–198.
- Neale, P.J., R.F. Davis, and J.J. Cullen. 1998. Interactive effects of ozone depletion and vertical mixing on photosynthesis of Antarctic phytoplankton. *Nature* 392: 585–589.
- Nebel, B., and J. Fuhrer. 1994. Inter- and intraspecific differences in ozone sensitivity in semi-natural plant communities. *Angewandte Botanik* 68: 116–121.
- Neilson, R.P. 1986. High-resolution climatic analysis and Southwest biogeography. *Science* 232: 27–34.
- Norby, R.J. 1987. Nodulating and nitrogenase activity in nitrogen-fixing woody plants stimulated by CO₂ enrichment of the atmosphere. *Physiologia Plantarum* 71: 77–82.
- Norton, L.R., A.R. McLeod, P.D. Greenslade, L.S. Firbank, and A.R. Watkinson. 1999. Elevated UV-B radiation effects on experimental grassland communities. *Global Change Biology* 5: 601–608.
- O'Brien, C.M., C.J. Fox, B. Planque, and J. Casey. 2000. Climate variability and North Sea cod. *Nature* 404: 142.
- Odum, E.P., J.T. Finn, and E.H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. *BioScience* 29: 349–352.
- Overpeck, J.T., P.J. Bartlein, and T. Webb. 1991. Potential magnitude of future vegetation change in eastern North America: Comparisons with the past. *Science* 254: 692–695.
- Owensby, C.E., J.M. Ham, A.K. Knapp, and L.A. Auen. 1999. Biomass production and species composition change in a tallgrass prairie ecosystem after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* 5: 497–506.
- Papadopoulos, Y.A., R.J. Gordon, K. McRae, R.S. Bush, G. Belanger, E.A. Butler, S.A.E. Fillmore, and M.M. Morrison. 1999. Current and elevated levels of UV-B radiation have few impacts on yields of perennial forage crops. *Global Change Biology* 5: 847–856.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J.K. Hill, C.D. Thomas, H. Descimon, B. Huntley, L. Kalla, J. Kulberg, T. Tammaru, W.J. Tennent, J.A. Thomas, and M. Warren. 1999. Poleward shifts in geographic ranges of butterfly species associated with regional warming. *Nature* 399: 576–583.
- Payette, S., and L. Filion. 1985. White spruce expansion at the tree line and recent climatic change. *Canadian Journal of Forest Research* 15: 241–251.
- Pearcy, R.W., and O. Bjorkman. 1983. Physiological effects. In E.R. Lemon (ed.), *CO₂ and Plants*, pp. 65–105. Boulder, Colo.: Westview Press.
- Peet, R. K. 1992. Community structure and ecosystem function. In D.C. Glenn-Lewin, R.K. Peet, and T.T. Veblen (eds.), *Plant Succession: Theory and Predictions*, pp. 103–151. London: Chapman and Hall.

- Pell, E.J., C.D. Schlagnhauer, and R.N. Artica. 1997. Ozone-induced oxidative stress: Mechanisms of action and reaction. *Physiologia Plantarum* 100: 264–273.
- Petchey, O.L., P.T. McPherson, T.M. Casey, and P.J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402: 69–72.
- Peterjohn, W.T., J.M. Melillo, F.B. Bowles, and P.A. Steudler. 1993. Soil warming and trace gas fluxes: Experimental design and preliminary flux results. *Oecologia* 93: 18–24.
- Peterjohn, W.T., J.M. Melillo, P.A. Steudler, K.M. Newkirk, F.P. Bowles, and J.D. Aber. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. *Ecological Applications* 4: 617–625.
- Petit, J.R., J. Jouzel, D. Raynaud, N.I. Barkov, J.-M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V.M. Kotyakov, M. Legrand, V.Y. Kipenko, C. Lorius, L. Pepin, C. Ritz, E. Saltzman, and M. Stievenard. 1999. Climate and atmospheric history of the past 430,000 years from the Vostok ice core, Antarctica. *Nature* 399: 429–438.
- Pitelka, L. F., J. Ash, S. Berry, R.H.W. Bradshaw, L. Brubaker, J.S. Clark, M.B. Davis, J.M. Dyer, R.H. Gardner, H. Gitay, G. Hope, R. Hengeveld, B. Huntley, G.A. King, S. Lavorel, R.N. Mack, G.P. Malanson, M. McGlone, I.R. Noble, I.C. Prentice, M. Rejmanek, A. Saunders, A.M. Solomon, S. Sugita, and M.T. Sykes. 1997. Plant migration and climate change. *American Scientist* 85:464–473.
- Pockman, W.T., and J.S. Sperry. 1997. Freezing-induced xylem cavitation and the northern limit of *Larrea tridentata*. *Oecologia* 109: 19–27.
- Poiani, K.A., and W.C. Johnson. 1991. Global warming and prairie wetlands. *BioScience* 41: 611–618.
- Polley, H.W., H.B. Johnson, and H.S. Mayeux. 1994. Increasing CO₂: Comparative responses of C4 grass *Schizachrium* and grassland invader *Prosopis*. *Ecology* 75: 976–989.
- Poorter, H. 1993. Interspecific variation in the growth responses of plants to an elevated ambient CO₂ concentration. *Vegetatio* 104/105: 77–97.
- Poorter, H. 1998. Do slow-growing species and nutrient-stressed plants respond relatively strongly to elevated CO₂? *Global Change Biology* 4: 693–697.
- Potvin, C., and L. Vasseur. 1997. Long-term CO₂ enrichment of a pasture community: Species richness, dominance and succession. *Ecology* 78: 666–677.
- Pough, F.H. 1976. Acid precipitation and embryonic mortality of spotted salamanders, *Ambystoma maculatum*. *Science* 192: 68–70.
- Price, M.V., and N.M. Waser. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79: 1261–1271.
- Price, M.V., and N.M. Waser. 2000. Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications* 10: 811–823.
- Rabalais, N.N., R.E. Turner, D. Justic, Q. Dortch, W.J. Wiseman, and B.K. Sen Gupta. 1996. Nutrient changes in the Mississippi River and system responses on the adjacent continental shelf. *Estuaries* 19: 386–407.
- Rapport, D.J., H.A. Regier, and T.C. Hutchinson. 1985. Ecosystem behavior under stress. *American Naturalist* 125: 617–640.

- Raven, J.A. 1994. Carbon fixation and carbon availability in marine phytoplankton. *Photosynthesis Research* 39: 259–273.
- Rebbeck, J. 1996. Chronic ozone effects on three northeastern hardwood species: Growth and biomass. *Canadian Journal of Forest Research* 26: 1788–1798.
- Rebbeck, J., U. Blum, and A.S. Heagle. 1988. Effects of ozone on the regrowth and energy reserves of a ladino clover-tall fescue pasture. *Journal of Applied Ecology* 25: 659–681.
- Reich, P.B. 1987. Quantifying response to ozone: A unifying theory. *Tree Physiology* 3: 573–577.
- Reid, C. 1899. *The Origin of the British Flora*. London: Dulau.
- Reid, C.D., and E.L. Fiscus. 1998. Effects of elevated $[CO_2]$ and/or ozone on limitations to CO_2 assimilation in soybean (*Glycine max*). *Journal of Experimental Botany* 49: 885–895.
- Reid, C.D., and B.R. Strain. 1994. Effects of CO_2 enrichment on whole-plant carbon budget of seedlings of *Fagus grandifolia* and *Acer saccharum* in low irradiance. *Oecologia* 98: 31–39.
- Reiling, K., and A.W. Davison. 1992. The response of native, herbaceous species to ozone: Growth and fluorescence. *New Phytologist* 120: 29–37.
- Reynolds, J.F., R.A. Virginia, P.R. Kemp, A.G. DeSoyza, and D.C. Tremmel. 1999. Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecological Monographs* 69: 69–106.
- Ries, G., W. Heller, H. Puchta, H. Sandermann, H.K. Seidlitz, and B. Hohn. 2000. Elevated UV-B reduces genome stability in plants. *Nature* 406: 98–101.
- Rind, D., R. Goldberg, J. Hansen, C. Rosenzweig, and R. Ruedy. 1990. Potential evapotranspiration and the likelihood of future drought. *Journal of Geophysical Research* 95: 9983–10004.
- Ringelberg, D.B., J.O. Stair, J. Ahmeida, R.J. Norby, E.G. O'Neill, and D.C. White. 1997. Consequences of rising atmospheric CO_2 levels for the belowground microbiota associated with white oak. *Journal of Environmental Quality* 26: 495–503.
- Ritchie, J. C., and G. M. MacDonald. 1986. The patterns of post-glacial spread of white spruce. *Journal of Biogeography* 13: 527–540.
- Robertson, D.M., R.A. Ragotzkie, and J.J. Magnuson. 1992. Lake ice records used to detect historical and future climatic changes. *Climatic Change* 21: 407–427.
- Roemmich, D., and J. McGowan. 1995. Climatic warming and the decline of zooplankton in the California current. *Science* 267: 1324–1326.
- Root, T. 1988. Energy constraints on avian distributions and abundances. *Ecology* 69: 330–339.
- Rosenzweig, M.L. 1971. Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time. *Science* 171: 385–387.
- Rothrock, D.A., Y. Yu., and G.A. Maykut. 1999. Thinning of the Arctic sea-ice cover. *Geophysical Research Letters* 26: 3469–3472.
- Roy, D.B., and T.H. Sparks. 2000. Phenology of British butterflies and climate change. *Global Change Biology* 6: 407–416.

- Rudorff, B.F.T., C.L. Mulchi, E.H. Lee, R. Rowland, and R. Rausch. 1996. Effects of enhanced O_3 and CO_2 enrichment on plant characteristics in wheat and corn. *Environmental Pollution* 94: 53–60.
- Rustad, L.E., and I.J. Fernandez. 1998. Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce-fir forest soil in Maine, USA. *Global Change Biology* 4: 597–605.
- Sadowsky, M.J., and M. Schortemeyer. 1997. Soil microbial responses to increased concentrations of atmospheric CO_2 . *Global Change Biology* 3: 217–224.
- Sagarin, R.D., J.P. Barry, S.E. Gilman, and C.H. Baxter. 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* 69: 465–490.
- Sageman, B.B., and C.R. Bina. 1997. Diversity and species abundance patterns in late Cenomanian black shale biofacies, western interior, U.S. *Palaaios* 12: 449–466.
- Sala, O.E., F.S. Chapin, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker, and D.H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.
- Samuelson, L.J., and J.M. Kelly. 1997. Ozone uptake in *Prunus serotina*, *Acer rubrum* and *Quercus rubra* forest trees of different sizes. *New Phytologist* 136: 255–264.
- Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283: 2095–2097.
- Santer, B.D., K.E. Taylor, T.M.I. Wigley, T.C. Johns, P.D. Jones, D.J. Karoly, J.F.B. Mitchell, A.H. Oort, J.E. Penner, V. Ramaswamy, M.D. Schwartzkopf, R.J. Stouffer, and S. Tett. 1996. A search for human influences on the thermal structure of the atmosphere. *Nature* 392: 39–46.
- Sasek, T.W. 1985. Implications of atmospheric carbon dioxide enrichment for the physiological ecology and distribution of two introduced woody vines, *Pueraria lobata* Ohwi (kudzu) and *Lonicera japonica* Thumb. (Japanese honeysuckle). Ph.D. dissertation, Duke University, Durham, N.C.
- Sasek, T.W., and B.R. Strain. 1988. Effects of carbon dioxide enrichment on the growth and morphology of kudzu (*Pueraria lobata*). *Weed Science* 36: 28–36.
- Sasek, T.W., and B.R. Strain. 1989. Effects of carbon dioxide enrichment on the expansion and size of kudzu (*Pueraria lobata*) leaves. *Weed Science* 37: 23–28.
- Sasek, T.W., and B.R. Strain. 1990. Implications of atmospheric CO_2 enrichment and climate change for the geographical distribution of two introduced vines in the USA. *Climatic Change* 16: 31–51.
- Sasek, T.W., and B.R. Strain. 1991. Effects of CO_2 enrichment on the growth and morphology of a native and introduced honeysuckle vine. *American Journal of Botany* 78: 69–75.
- Schimel, D., I.G. Enting, M. Heimann, T.M.L. Wigley, D. Raynaud, D. Alves, and U. Siegenthaler. 1995. CO_2 and the carbon cycle. In J.T. Houghton, L.G. Meira Filho, J. Bruce et al. (eds.), *Climate Change 1994*, pp. 35–71. Cambridge: Cambridge University Press.

- Schindler, D.W. 1988. Effects of acid rain on freshwater ecosystems. *Science* 239: 149–157.
- Schindler, D.W., K.G. Beaty, E.J. Fee, D.R. Cruikshank, E.R. DeBruyn, D.L. Findlay, G.A. Linsey, J.A. Shearer, M.P. Stainton, and M.A. Turner. 1990. Effects of climatic warming on lakes of the central boreal forest. *Science* 250: 967–970.
- Schlesinger, W.H. 1997. *Biogeochemistry: An Analysis of Global Change*. 2nd ed. San Diego: Academic Press.
- Schortemeyer, M., U.A. Hartwig, G.R. Hendrey, and M.J. Sadowsky. 1996. Microbial community changes in the rhizospheres of white clover and perennial ryegrass exposed to Free Air Carbon Dioxide Enrichment (FACE). *Soil Biology and Biochemistry* 28: 1717–1724.
- Searles, P.S., S.D. Flint, S.B. Diaz, M.C. Rousseaux, C.L. Ballare, and M.M. Caldwell. 1999. Solar ultraviolet-B radiation influence on *Sphagnum* bog and *Carex* fen ecosystems: First field season findings in Terra del Fuego, Argentina. *Global Change Biology* 5: 225–234.
- Shärky, L., H. Ro-Poulsen, F.A.M. Wellburn, and L.J. Sheppard. 1998. Impacts of ozone on forests: A European perspective. *New Phytologist* 139: 109–122.
- Smith, R.C., B.B. Prezelin, K.S. Baker, R.R. Bidigare, N.P. Boucher, T. Coley, D. Karentz, S. MacIntyre, H.A. Matlick, D. Menzies, M. Ondrusek, Z. Wan, and K.J. Waters. 1992. Ozone depletion: Ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science* 255: 952–959.
- Sorensen, L.G., R. Goldberg, T.L. Root, M.G. Anderson. 1998. Potential effects of global warming on waterfowl populations breeding in the northern Great Plains. *Climatic Change* 40: 343–369.
- Spivack, A.J., C.-F. You, and H.J. Smith. 1993. Foraminiferal boron isotope ratios as a proxy for surface ocean pH over the past 21 Myr. *Nature* 363: 149–151.
- Stoddard, J.L., D.S. Jeffries, A. Lukewille, T.A. Clair, P.J. Dillon, C.T. Driscoll, M. Forsius, M. Johannessen, J.S. Kahl, J.H. Kellogg, A. Kemp, J. Mannio, D.T. Monteith, P.S. Murdoch, S. Patrick, A. Rebsdorf, B.L. Skjelkvale, M.P. Stainton, T. Traaen, H. van Dam, K.E. Webster, J. Wieting, and A. Wilander. 1999. Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* 401: 575–578.
- St. Omer, L., and S.M. Horvath. 1983. Elevated CO₂ atmospheres and whole plant senescence. *Ecology* 64: 1311–1314.
- Street-Perrott, F. A., Y. Huang, R.A. Perrott, G. Eglinton, P. Barker, L.B. Khelifa, D.D. Harkness, and D.O. Olago. 1997. Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. *Science* 278:1422–1426.
- Sullivan, J.H., and A. H. Teramura. 1992. The effects of ultraviolet-B radiation on loblolly pine. 2. Growth of field-grown seedlings. *Trees* 6: 115–120.
- Taberlet, P., L. Fumagalli, A.G. Wust-Saucy, and J.-F. Cossons. 1998. Comparative phylogeography and post-glacial colonization routes in Europe. *Molecular Ecology* 7:453–464.
- Taylor, K.C., P.A. Mayewski, R.B. Alley, E.J. Brook, A.J. Gow, P.M. Grootes, D.A. Meese, E. S. Saltzman, J. P. Severinghaus, M. S. Twickler, J. W. C. White, S. Whitlow, and G. A. Zielinski. 1997. The Holocene-Younger Dryas transition recorded at Summit, Greenland. *Science* 278:825–827.

- Tett, S.F.B., P.A. Stott, M.R. Allen, W.J. Ingram, and J.F.B. Mitchell. 1999. Causes of twentieth-century temperature change near the earth's surface. *Nature* 399: 569–572.
- Thomas, C.D., and J.J. Lennon. 1999. Birds extend their ranges northwards. *Nature* 399:213.
- Thomas, R.B., D.D. Richter, H. Ye, P.R. Heine, and B.R. Strain. 1991. Nitrogen dynamics and growth of seedlings of an N-fixing tree (*Gliricidia sepium* [Jadq.] Walp.) exposed to elevated atmospheric carbon dioxide. *Oecologia* 88: 415–421.
- Thompson, A.M., M.A. Huntley, and R.W. Stewart. 1990. Perturbations to tropospheric oxidants, 1985–2035. 1. Calculations of ozone and OH in chemically coherent regions. *Journal of Geophysical Research* 95: 9829–9844.
- Tilman, D. 1982. *Resource Competition and Community Structure*. Princeton, N.J.: Princeton University Press.
- Tipping, E., T.R. Carrick, M.A. Hurley, J.B. James, A.J. Lawlor, S. Lofts, E. Rigg, D.W. Sutcliffe, and C. Woof. 1998. Reversal of acidification in upland waters of the English Lake District. *Environmental Pollution* 103: 143–151.
- Tissue, D.T., J.P. Megonigal, and R.B. Thomas. 1997. Nitrogenase activity and N_2 fixation are stimulated by elevated CO_2 in a tropical N_2 fixing tree. *Oecologia* 109: 28–33.
- Tissue, D.T., R.B. Thomas, and B.R. Strain. 1997. Atmospheric CO_2 enrichment increases growth and photosynthesis of *Pinus taeda*: A 4-year experiment in the field. *Plant Cell and Environment* 20: 1123–1134.
- Tousignant, D., and C. Potvin. 1996. Selective responses to global change: Experimental results on *Brassica juncea* (L.) Czern. In C. Korner and F.A. Bazzaz (eds.), *Carbon Dioxide, Populations, and Communities*, pp. 23–30. San Diego: Academic Press.
- Tucker, C.J., W.W. Newcomb, and H.E. Dregne. 1994. AVHRR data sets for determination of desert spatial extent. *International Journal of Remote Sensing* 15: 3547–3565.
- Turner, R.E., and N.N. Rabalais. 1991. Changes in Mississippi River water quality this century. *BioScience* 41: 140–147.
- Turner, R.E., and N.N. Rabalais. 1994. Coastal eutrophication near the Mississippi River delta. *Nature* 368: 619–621.
- Van Devender, T.R., and W.G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. *Science* 204: 701–710.
- Vasseur, L., and C. Potvin. 1998. Natural pasture community response to enriched carbon dioxide atmosphere. *Plant Ecology* 135: 31–41.
- Visser, M.T., A.J. van Noordwijk, J.M. Tinbergen, and C.M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London* 265: 1867–1870.
- Vitousek, P.M., J.D. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger, and D.G. Tilman. 1997. Human alteration of the global nitrogen cycle: Sources and consequences. *Ecological Applications* 7: 737–750.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468–478.

- Volin, J.C., P.B. Reich, and T.J. Givnish. 1998. Elevated carbon dioxide ameliorates the effects of ozone on photosynthesis and growth; species respond similarly regardless of photosynthetic pathway or plant functional group. *New Phytologist* 138: 315–325.
- Volz, A., and D. Kley. 1988. Evaluation of the Montsouris series of ozone measurements made in the nineteenth century. *Nature* 332: 240–242.
- Walker, D., and Y. Chen. 1987. Palynological light on tropical rainforest dynamics. *Quaternary Science Reviews* 6: 77–92.
- Walker, R.F., D.R. Geisinger, D.W. Johnson, and J.T. Ball. 1995. Enriched atmospheric CO₂ and soil P effects on growth and ectomycorrhizal colonization of juvenile ponderosa pine. *Forest Ecology and Management* 78: 207–215.
- Walters, M.B., and P.B. Reich. 1996. Are shade tolerance, survival and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology* 77: 841–853.
- Walters, M.B., and P.B. Reich. 2000. Trade-offs in low-light CO₂ exchange: A component of variation in shade tolerance among cold temperate tree seedlings. *Functional Ecology* 14: 155–165.
- Ward, J.K. and B.R. Strain. 1997. Effects of low and elevated CO₂ partial pressures on growth and reproduction of *Arabidopsis thaliana* from different elevations. *Plant Cell and Environment* 20: 254–260.
- Ward, J.K., B.R. Strain, J. Antonovics, and R.B. Thomas. 2000. Is atmospheric CO₂ a selective agent on model C3 annuals? *Oecologia* 123: 330–341.
- Warner, M.E., W.K. Fitt, and G.W. Schmidt. 1999. Damage to photosystem II in symbiotic dinoflagellates: A determinant of coral bleaching. *Proceedings of the National Academy of Sciences USA* 96: 8007–8012.
- Warwick, K.R., and G. Taylor. 1995. Contrasting effects of tropospheric ozone on five native herbs which coexist in calcareous grassland. *Global Change Biology* 1: 143–151.
- Warwick, K.R., G. Taylor, and H. Blum. 1998. Biomass and compositional changes occur in chalk grassland turves exposed to elevated CO₂ for two seasons in FACE. *Global Change Biology* 4: 375–385.
- Wayne, P. M., and F. A. Bazzaz. 1995. Seedling density modifies the growth responses of yellow birch maternal families to elevated carbon dioxide. *Global Change Biology* 1: 315–324.
- Wayne, P. M., and F. A. Bazzaz. 1997. Light acquisition and growth by competing individuals in CO₂ enriched atmospheres: Consequences for size structure in regenerating birch stands. *Journal of Ecology* 85: 29–42.
- Webb, S. L. 1987. Beech range extension and vegetation history: Pollen stratigraphy of two Wisconsin lakes. *Ecology* 68:1993–2005.
- Wedin, D.A., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. *Science* 274: 1720–1723.
- Wentz, F.J., and M. Schabel. 2000. Precise climate monitoring using complementary satellite data sets. *Nature* 403:414–416.
- Westman, W.E. 1979. Oxidant effects on California coastal sage scrub. *Science* 205: 1001–1003.

- White, T.A., B.D. Campbell, P.D. Kemp, and C.L. Hunt. 2000. Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. *Global Change Biology* 6: 671–684.
- Whitfield, C.P., A.W. Davison, and T.W. Ashenden. 1997. Artificial selection and heritability of ozone resistance in two populations of *Plantago major*. *New Phytologist* 137: 645–655.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.
- Willems, J.H., and R.K. Peet. 1993. Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science* 4: 203–212.
- Williams, W.E., K. Garbutt, F.A. Bazzaz, and P.M. Vitousek. 1986. The response of plants to elevated CO₂. IV. Two deciduous forest tree communities. *Oecologia* 69: 454–459.
- Woods, K. D., and M. B. Davis. 1989. Paleoecology of range limits: Beech in the upper peninsula of Michigan. *Ecology* 70:681–696.
- Wright Jr., H. E., J. E. Kutzbach, T. Webb III, W. F. Ruddiman, F. A. Street-Perrott, and P. J. Bartlein. 1993. *Global Climates since the Last Glacial Maximum*. Minneapolis: University of Minnesota Press.
- Yakimchuk, R., and J. Hoddinott. 1994. The influence of ultraviolet-B light and carbon dioxide enrichment on the growth and physiology of three conifer species. *Canadian Journal of Forest Research* 24: 1–8.
- Yeates, G.W., P. Newton, and D.J. Ross. 1999. Responses of soil nematode fauna to naturally elevated CO₂ levels influenced by soil pattern. *Nematology* 1: 285–293.
- Zak, D.R., D.B. Ringelberg, K.S. Pregitzer, D.L. Randlett, D.C. White, and P.S. Curtis. 1996. Soil microbial communities beneath *Populus grandidentata* grown under elevated atmospheric CO₂. *Ecological Applications* 6: 257–262.
- Zak, D.R., K.S. Pregitzer, P.S. Curtis, and W.E. Holmes. 2000. Atmospheric CO₂ and the composition and function of soil microbial communities. *Ecological Applications* 10: 47–59.
- Zaller, J.G., and J.A. Arnone. 1999. Earthworm responses to plant species loss and elevated CO₂ in calcareous grassland. *Plant and Soil* 208: 1–8.
- Zogg, G.P., D.R. Zak, D.B. Ringelberg, N.W. MacDonald, K.S. Pregitzer, and D.C. White. 1997. Compositional and functional shifts in microbial communities due to soil warming. *Soil Science Society of America Journal* 61: 475–481.

MAKING SMART CONSERVATION DECISIONS

H. P. Possingham, S. J. Andelman,
B. R. Noon, S. Trombulak, and H. R. Pulliam

In little more than a decade, conservation biology has generated a large and growing body of theory aimed at predicting and managing the impacts of anthropogenic activities on populations, species, and ecosystems (e.g., Meffe and Carroll 1997; Ferson and Burgman 2000). However, to succeed in its mission, conservation biology must do more than generate theories and principles. Conservation biologists must use their theories to deliver effective, science-based decision tools for practical use by managers and policy makers. Furthermore, to demonstrate the efficacy of conservation biology theory and applications to skeptical managers, conservation biologists must also establish feasible yet reliable monitoring programs to detect key trends and effects and determine the effectiveness of decisions (Kareiva et al. 1999; Simberloff 1999). Transforming pure science—whether theoretical or empirical—into information that can actually be used by managers and decision makers to address the sorts of conservation problems outlined throughout this volume remains a major challenge in conservation biology. To meet this challenge, the next generation of conservation biologists will need to embrace more economics, more management science, more decision theory, and more operations research.

This chapter has two broad objectives. First, we outline the key elements for how to make smart conservation decisions and measure their benefits—an outline that is applicable to the sorts of conservation problems discussed in

this book. With this framework in mind, we then highlight priorities and directions for future research.

We begin by discussing some specific problems generic to species and ecosystem management that have resisted rational, science-based solutions. These examples illustrate some of the gaps in traditional approaches to conservation biology research and provide a platform to illustrate the benefits of decision-theory approaches. Next we give examples of the application of decision theory to solving conservation problems. While decision-making methods can account for uncertainty and errors, monitoring the results of conservation actions is essential for improved decision making in the future.

Ultimately, our objective is to encourage the development of active adaptive management programs on real conservation problems (Parma et al. 1998). Within an adaptive management framework, once an action has been initiated, a monitoring program must be implemented that evaluates and measures the performance of that action. The performance evaluation then informs the decision-making process by reducing uncertainty and ignorance. In this paper we use the term *monitoring* to refer to a repeated assessment of some environmental attribute for the purpose of detecting change within a defined area over time (Thompson et al. 1998). Specifically, the type of monitoring we describe is “performance evaluation.” That is monitoring explicitly designed to assist decision making and management. We conclude with an overview of research opportunities for monitoring and decision making, emphasizing the challenge of developing robust rules of thumb for making decisions.

Where Conservation Biology Has Failed to Provide Useful Advice

Where in space should habitat be protected from destruction, and where should it be restored? This question is fundamental to conservation, and conservation biology should provide the answer. A range of theories generally addresses this question, beginning with “island biogeography theory” (MacArthur and Wilson 1967) and continuing more recently with “metapopulation theory” (Hanski 1999) and “source-sink theory” (Pulliam 1988). Let us see what answers these theories provide to this question.

Island biogeography theory generated a series of rules, most notably:

- big reserves are better than small reserves; and
- connected (or close) reserves are better than unconnected reserves.

Metapopulation theory tells us that there are several ways to increase the likelihood that a metapopulation will persist:

- decrease local extinction rates;
- increase between-patch colonization rates;
- increase the number of suitable patches (or, conversely, minimize patch loss); and

- increase the number of occupied patches.

Source-sink theory emphasizes the importance of identifying habitat where population growth rates are consistently positive, hence the rule: Protect source populations and ignore sink populations.

We also have the empirically derived rule: Reserves with a low edge-to-area ratio are better than reserves with a high edge-to-area ratio.

All these rules have been useful in providing general conservation principles, but their use is more limited for dealing with specific conservation and management problems. To provide useful practical advice, conservation biologists must have a clear understanding of the questions that managers want answered. For example, consider the question of where it is best to restore habitat. A land manager interested in habitat restoration will typically have a finite set of resources and financial constraints. She may envisage revegetating 10 percent of an existing site. The question for conservation biologists is: Which 10 percent should be restored to maximize biodiversity benefits?

Let us assume that two patches of native vegetation exist on the site, one larger than the other. The specific question then is: To which of the following options should revegetation efforts be directed?

1. Make the bigger patch bigger.
2. Make the smaller patch bigger.
3. Connect the two patches with a broad corridor.
4. Make one new large patch.
5. Make many new small patches evenly scattered over the property.

Island biogeography theory and metapopulation theory provide few insights to help us choose among these options, except, perhaps, ruling out option 5—although without further information about the distribution of species and communities across the property, we might not want to eliminate that option. The reason these conservation biology theories have limited utility for such practical decisions is that the general principles have not been couched within a decision-making framework. The question of where to focus restoration efforts raises the immediate question of what biodiversity the land manager is trying to maintain or recover. What is the objective? A simple question that is rarely answered.

Even when an explicit objective is specified, none of our theories provide explicit predictions as to how that objective is most likely to be met. If the biodiversity objective is to minimize the likelihood of a species becoming extinct, we might test alternative habitat reconstruction scenarios in a population viability model (something that is rarely done given the lack of data and the demands on the time of managers). If the biodiversity objective is to restore a representative sample of habitats, then information on soil types and topog-

raphy would be vital. Given the vast conservation literature on habitat fragmentation generated over the past decade, it is an embarrassment that so little of this research (empirical or theoretical) provides answers to the most basic practical questions concerning optimal habitat reconstruction for biodiversity conservation. The theories generate a list of generally useful things we might do, but they offer little insight into how best to choose among the alternative options (Possingham 1997).

The example provided is deliberately simple. Most conservation problems are more complex, and a land manager may envisage spending her conservation dollars in other nature conservation activities, such as control of introduced predators and weeds in the existing habitat patches. The question then becomes: What fraction of our conservation effort should be directed to each of several management activities: revegetation, predator control, and weed control? What conservation biology theory helps us juggle these alternatives?

A second common question in conservation biology relates to the problem of reintroductions and captive breeding. A large amount of science is focused on reintroduction and captive breeding (Ralls and Ballou 1986), but few protocols exist for answering basic questions like:

- When, in the decline of a threatened species, should we initiate a captive breeding program?
- How many individuals should be brought in to found a captive breeding program?
- Which individuals should constitute the initial captive population (i.e., what combination of ages and sexes)?
- When should individuals be released into the wild, and how many?

Again, the existing theory provides general rules, such as: reintroduction of a large number of individuals will typically be better than a smaller reintroduction. Empirical reintroduction research yields essential data and experience but provides only a limited framework for extending experience with a particular species or site to new species or uncertain circumstances. Maguire et al. (1987), Maguire and Servheen (1992), and Lubow (1996) address some of these reintroduction and captive breeding questions for specific circumstances using decision-theory tools, but they are lonely beacons.

Decision Theory and How It Has Been Used in Conservation

Decision theory is a framework within which people responsible for management attempt to achieve explicitly stated objectives while acknowledging the levels of uncertainty involved with the decision process (Clemen 1996). Other professionals such as engineers (Kulkarni et al. 1993; Ravirala and Grivas 1995; Teng and Tzeng 1996) and financial advisers (Beenhakker 1975) use this sort of theory to make decisions. In some cases decision theory

relies on complex mathematical tools that go under the generic name of “mathematical programming methods.” However decision theory can be much broader and often includes qualitative tools such as “ecological risk assessment” or “multicriteria decision analysis.” The common thread within the theory is a disciplined protocol for problem solving that includes the following seven steps (Shea et al. 1998):

1. Specify the management objectives, or at least list the indicators of policy performance (e.g., minimize the risk that numbats become extinct in the next fifty years). Where there are multiple objectives, utility theory (Maguire and Servheen 1982; Guikema and Milke 1999) is employed to deal with the problem of how to maximize multiple objectives that are measured in different currencies (e.g. money, biodiversity loss, and risk to human health).
2. List the management options and express them as control variables (e.g., release x animals in year t , expend y on baiting predators, etc.).
3. Specify the variables that describe the state of the system (e.g., population size, predator abundance).
4. Develop a conceptual model of the dynamics of the system being managed, and if possible develop equations to describe the dynamics of the state variables (e.g., equations for numbat and predator population codynamics). This step will often involve collaboration between a field biologist and an ecological modeler.
5. Specify constraints that bound the decision variables and state variables (e.g., a recovery program budget, the social acceptability of predator reduction strategies, etc.).
6. Specify the range of uncertainty for all the parameters.
7. Find solutions to the problem. Once the problem is defined by these components the manager may often need a decision-making protocol and/or mathematical programming package to find the best, or at least some good, solutions.

To illustrate how decision-theory thinking might be integrated with traditional conservation biology approaches, we now present three examples.

Example 1: Optimal Fire Management for a Large Conservation Park

Managing disturbance processes in conservation areas is a contentious issue throughout the world. In many large and seminatural terrestrial systems fire is the main force that disturbs vegetation, and it is often managed with fuel reduction burning, attempts to reduce ignition frequency, and prescribed burning to increase fire frequency. The pro- and anti-fire advocates often take highly polarized positions based on preconceived ideas, conflicting goals, and nonpredictive mental models of an area's natural history. The fear

of making the wrong decision invariably means we make the decision to do nothing.

Here we summarize Richards et al.'s (1999) use of decision theory to determine an optimal fire management strategy for a large conservation reserve. The description of the problem fits into the seven-point framework above:

1. *Statement of objective(s).* Richards et al. set the broad objective of maintaining a balance of the different successional states. Specifically, they set the target that at least 20 percent of the park should be in each of the three successional states of the vegetation—early, mid, and late. (This is a surrogate objective for the more fundamental objective of minimizing species loss. However, there are so many species, and limited information on each, that the ecosystem-level objective is expedient and more likely to be implemented and monitored.)
2. *List of management options.* Each year the park manager has three options: do nothing, attempt to stop all wild fires, and prescribe burns in some of the park.
3. *State variables.* The state of the system is the percentage of the park in each of the three successional states—early, mid, and late.
4. *State dynamics.* Using basic probability theory, Richards et al. constructed transition probabilities that predicted the chance of the park moving from any one state to any other state in a single year, given that the manager had chosen a particular management option for that year. The two forces that drove the dynamics were fire and vegetation succession, and the final state dynamics model is a Markov chain model.
5. *Constraints.* Richards et al. did not constrain the ability of the manager to enact any of the three management options, although they did assume that the fire suppression option would not be completely effective.
6. *Uncertainty.* Richards et al. varied the definition of early-, mid-, and late-successional habitat, and the relationship between fire frequency and habitat state, to do a limited test of the robustness of their conclusions. For more detailed fire management, a whole host of uncertainties regarding ability to control fire, risk to life and property, and even variability in the political climate, could be used to enhance the robustness of the results.
7. *Solution methods.* Richards et al. used stochastic dynamic programming, a common mathematical programming method (Intriligator 1971), to find the optimal solution.

The main outcome was a state-dependent fire management diagram that tells a manager what to do given a particular state of the park (see figure 10.1, from Possingham and Shea 1999). Where the resources to explore options for a particular park are limited, figure 10.1 *could* be thought of as a rough rule of thumb for fire management in a large seminatural park, although its robustness would require considerable further testing (see point 6 above).

Unexpectedly, Richards et al. found that a manager often needs to do something even when the park is in a “good” state, and sometimes a manager should do nothing when the park is in a “bad” state. Exactly when a manager should take no action is not easy to predict without a model. The stochastic dynamic programming method is able to accurately integrate decisions in a stochastic world over a longer time frame than human intuition can. There is no fixed optimal policy—it depends on the state of the park.

One question raised by the work was the social and economic cost of adopting different policies. This was not dealt with in detail, yet it may be important in some cases. Utility theory would need to be applied to generate relationships between different “values”—conservation value, economic

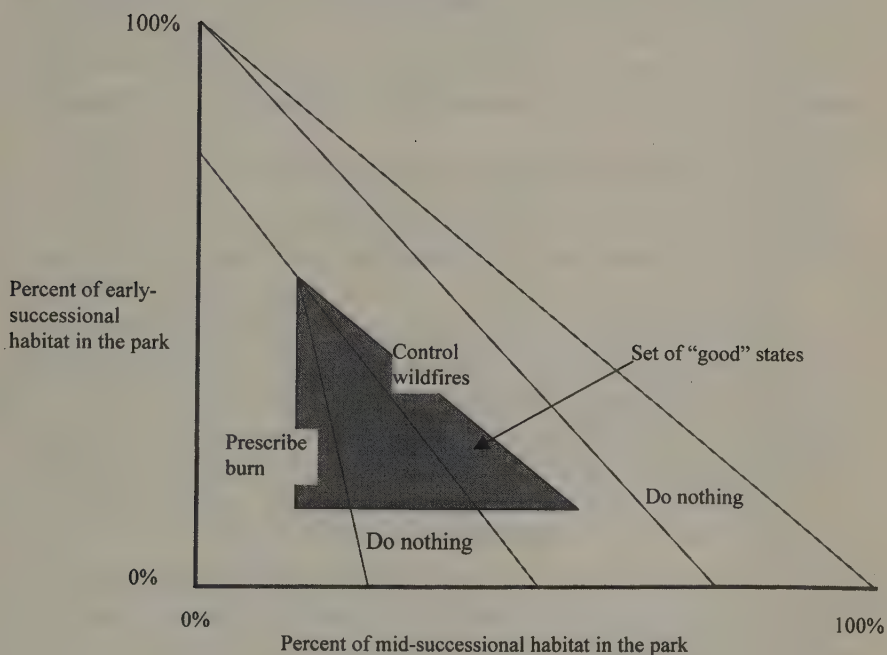


FIGURE 10.1. A state-dependent decision diagram for fire management in a large conservation reserve. The result is based on an objective of trying to keep at least 20 percent of the park in each of the three successional states—early, mid, and late. “Do nothing,” means that fires are neither started nor extinguished. From Possingham and Shea (1999).

cost, and social perception of fire. This issue is discussed in the context of another example below.

Example 2: Conservation Program Planning

Guikema and Milke (1999) consider the problem of allocating funds between different conservation projects. They use decision analysis to show how an agency would go about fund allocation. This use of decision theory is at quite a different scale from the example above and relies heavily on resource allocation theory developed in other industries. The work is briefly described below.

Envisage an agency that needs to allocate funds between a variety of projects. For example, it may be a federal agency that must decide how to allocate funds among one hundred projects on different threatened species, or it may be a nongovernmental organization that must decide how much money to invest in acquisition of new protected areas vs. how much to invest in management and restoration of existing reserves. Guikema and Milke (1999) summarize the conservation program planning procedure using a single diagram (figure 10.2).

Again we frame the problem in our seven-step outline:

1. *Statement of objective(s).* A typical agency-based management objective will represent a balance between recreation and biodiversity objectives, such as: number of visitor days, level of visitor satisfaction, species protection, and ecosystem protection. Much of Guikema and Milke (1999) is devoted to defining a utility function for each objective and combining them into one objective function. They show how some probability is required to modify the value of different objectives where the chance they will occur is uncertain. For species protection this might require some population viability analysis (Beissinger and Westphal 1998). For an objective such as number of visitor days this may require some expert judgment and statistical modeling.
2. *List of management options.* The decision is how to allocate the total budget among the projects. The control variables will be the amount of money allocated to each project.
- 3 and 4. *State variables and their dynamics.* The relationship between the funds allocated to each project and the achievement of each objective needs to be modeled. Often this requires submodels that may include expert opinion. These submodels will incorporate definitions of state dynamics, state variables, and the impact of funding allocation on the state variables and dynamics.
5. *Constraints.* The primary constraint is the total budget. The sum of the allocated funds must be less than, or equal to, the total budget. The user may wish to allocate varying amounts of funds to each project or just allow a project to occur, or not, with one fixed budget.

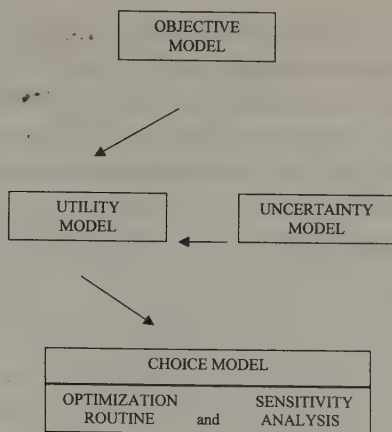


FIGURE 10.2. Components of the proposed conservation program planning procedure. From Guikema and Milke (1999).

6. *Uncertainty.* Systematically changing uncertain parameters would involve modifying the weights given to different objectives, or the parameters determined by expert opinion, etc.
7. *Solution methods.* In this case, the problem is linear (the objective function is a linear combination of the control variables, as are the constraints), so many standard mathematical programming packages can solve this problem quickly (even with a spreadsheet).

Guikema and Milke (1999) focused most of their discussion on step 1, framing the objective using multicomponent decision analysis. This task in government agencies is extremely complex and should include a wide range of social and human management issues that we have glossed over. While the scale and scope of this problem is quite different from that of example 1, we can apply the same seven-step framework.

Example 3: Reserve System Design

There is now a large literature on optimal reserve system design (Margules and Pressey 2000). Some of the problem formulation approaches and mathematics involved are reviewed in Possingham et al. (2000). Most ecologists are aware of the problem that is outlined in the seven-step decision-theory framework below; the social and economic aspects of reserve system design are in most need of further research:

1. *Statement of objective(s).* The objective is to adequately represent a suite of biodiversity features (usually species or habitat types) in a reserve system for the minimum cost. The minimum cost could be expressed in terms of the area, land cost, opportunity cost for other uses, management cost, and/or boundary length of the entire reserve system eventually chosen.

2. *List of management options.* The control options are to acquire, or not, each parcel of land or sea (called a planning unit) for the reserve system. There is a control variable for each planning unit. Current interest in off-reserve conservation and marine zoning would mean that the list of options for any parcel of land or sea should be broader and include nonpurchase options (like covenanting) or partial protection (through zoning).
3. *State variables.* This is usually a static problem where the key parameters are whether or not a biodiversity feature occurs in a planning unit.
4. *State dynamics.* There are normally no dynamics in reserve design problems, although this is an area of active research.
5. *Constraints.* The primary constraints are the biodiversity constraints. Usually the problem is formulated so that all biodiversity feature targets (e.g., conserve 15 percent of habitat A, or 500 individuals of species B) must be met. Planning units are constrained to one of a few states: already in the reserve system, available for conservation designation, or unavailable. Where we are interested in multi-use zoning of a region (e.g., the Great Barrier Reef Marine Park), a planning unit could be allocated to one of many zones.
6. *Uncertainty.* What happens if some of the GIS data layers have errors, or species lists are incomplete and inaccurate? Recent work (Andelman and Meir in press; Meir and Andelman in press) has been carried out on the impacts of uncertain, incomplete, or unreliable data.
7. *Solution methods.* These sorts of problems often become so large that classical mathematical programming methods fail. Simple heuristic algorithms or less classical optimization methods like simulated annealing have been used (Possingham et al. 2000).

Where reserve system design is implemented, it quickly becomes apparent that society is not a single entity with a single value system. Whereas a conservationist may value a particular site because it contains habitat for an endangered species, a timber company may value that site because of the potential revenue that might be generated from harvesting trees, while a horse-riding group may value that site for its recreational values. Perhaps one of the greatest benefits of decision theory is that it provides a protocol to help distinguish among, and integrate, various goals held by multiple sectors of the public.

For example, for the Great Barrier Reef Marine Park Possingham and colleagues are working on designing a reserve system to conserve representative samples of about eighty marine habitats and reefs in a fully protected zone. If conserving biodiversity is all that matters, this problem is hard, but not as hard as a problem that takes into account other values. Real-world marine

reserve design has to include the interests of others: commercial fishers, recreational fishers, the tourist industry, etc. Another complication for reserve system design is multiple zoning, where any planning unit needs to be assigned to one of several zones, each of which has implications for conservation, scientific, social, and economic use. Multiple zoning problems raise many questions. From the biodiversity perspective, would two reefs closed for fishing but not tourism compensate for one reserved reef opened up for fishing? A question like this is hard to answer for a single species, let alone for biodiversity in its entirety. We are a long way from developing fully integrated and adaptive reserve system planning tools, yet most countries need them now.

The reader will have noticed that the seven steps to decision making fall short of taking action. Two further essential steps now need to be considered, enacting the consequences of the decision making and then monitoring their consequences. Monitoring and consequent reevaluation and reformulation of our underlying data and models should lead us to the cycle of active adaptive management.

Monitoring and Performance Evaluation

Once a decision has been made, a monitoring program needs to be implemented, with the aim of evaluating and refining the solution or management action chosen. Ideally, the monitoring targets biodiversity assets and processes of greatest concern and uncertainty. Although monitoring activities are widespread in conservation biology and applied ecology, data from existing monitoring programs are underused for a number of reasons:

- many monitoring programs are poorly designed (e.g., the questions they are intended to answer are not well defined, and/or the methods selected are inappropriate to the objectives), resulting in suboptimal data;
- the spatial and temporal scales of monitoring activities are frequently inappropriate to the scales at which inferences from those monitoring activities are made;
- statistical and technological tools for analyzing monitoring data remain relatively primitive;
- little is known about the population and natural history needs of the organisms of concern; and
- there is a perception, particularly among agencies, that data collection, rather than analysis and communication of trends and patterns in those data, is the goal of monitoring.

Detecting ecologically meaningful trends and distinguishing the effects of human activities from those of natural disturbances—particularly at large

scales—are notoriously difficult (Dayton et al. 1998; Bradshaw et al. in review). Recent controversies over the magnitude and causes of declines of neotropical migratory songbirds (e.g., James et al. 1996; Thomas 1996) and amphibians (Blaustein et al. 1994; Alford and Richards 1999 and references therein) illustrate some of these difficulties. Furthermore, historically, monitoring has not been viewed as a legitimate research activity by many academic institutions, and maintaining adequate funding for monitoring over the requisite temporal and spatial scales has been difficult. Nevertheless, there is no way around the fact that successful management of biodiversity requires substantial monitoring.

Just as the common thread within decision theory involves a disciplined protocol consisting of seven steps, designing an effective monitoring program also involves a series of seven systematic steps (Mulder et al. 1999):

1. Specify goals.
2. Identify stressors.
3. Develop conceptual model.
4. Select indicators.
5. Establish sampling design.
6. Define methods of analysis.
7. Ensure link to decision making.

Below we briefly discuss each of these stages, highlighting key steps as well as areas where more research is needed.

Specify Goals

As discussed in the context of decision making, many conservation projects go wrong at this step. The same is true of monitoring projects. We cannot emphasize enough the importance of providing an explicit statement of the questions the monitoring program is intended to answer. Without such a statement, it is impossible to evaluate the effectiveness of the monitoring program.

Identify Stressors and Develop Conceptual Model

A conceptual model provides an overview of scientific understanding of how the ecosystem or population works and the state variables that describe the system. This knowledge is used to determine what measures of system performance are likely to be useful. The conceptual model should also include the effects of natural and human-induced stressors on the system. Measurements and inferences to biological systems are affected by the scale of observation, thus the temporal and spatial scales at which processes operate and

populations and communities respond must be estimated and clearly identified in the conceptual model (Noon et al. 1999).

Select Indicators and Establish Sampling Design

No monitoring design can feasibly encompass all ecological processes and species (Bradshaw et al. in review). Therefore, the design of monitoring programs requires careful consideration of candidate species and processes for measurement. Selection of variables should be made in the light of the overall goals and underlying conceptual model of the ecosystem of interest (NRC 2000). Although biodiversity has many dimensions, since we are limited in the number of things we can measure, and there is pressure for quick answers, it is popular to rely on monitoring surrogates such as indicators, keystones, and umbrella species (Landres et al. 1988; Simberloff 1998; Andelman and Fagan 2000).

Despite their popularity, particular umbrella and indicator species have often been chosen as management and monitoring surrogates without adequate testing of their performance (Simberloff 1998; Caro and O'Doherty 1999). This, in turn has led to confusion about when a species is being monitored for its own sake, and when a species can appropriately function as an accurate indicator of other organisms or environmental attributes. Where the performance of surrogates has been evaluated, results suggest that the utility of existing approaches to selecting surrogates is limited and almost certainly scale dependent (Andelman and Fagan 2000; Williams et al. in press). Another analysis, focusing on the northern spotted owl, suggests that that species may act as an adequate habitat surrogate for many other species (Noon and Bingham in press).

Despite concerns, the fact remains that it is impossible to assess the status and trend of all species of interest and that some surrogate-based approach is necessary. In addition, some land management agencies, such as the U.S. Forest Service, are legally required to use "management indicator species" to assess the impacts of any proposed management action on the system as a whole. This reality led a recent committee of scientists to propose the use of focal species, defined as those species whose status and trend allow insights into the integrity of the larger ecological system to which they belong. However, the committee noted that currently there is no definitive algorithm for unambiguously identifying focal species. This remains a priority area for accelerated ecological research.

Define Methods of Analysis and Ensure Link from Monitoring to Decision Making

For monitoring programs to be useful they must be efficient, informative, and reliable (Thomas 1996). For example, given an objective of detecting a

population decline and a fixed level of effort or resources, how many sites should be monitored? How many samples are required to detect a trend in population size when there is uncertainty in observations and significant environmental variation? How likely is it that a particular sampling procedure will detect a rare species?

Most frequently used statistical techniques do not answer these questions because they are rooted in the tradition of null-hypothesis testing. Typical management programs hinge on the implicit assumption that if no problem is observed, none exists. The burden of proof rests with monitoring programs. If a monitoring program fails to detect a trend or a rare species, that impact is assumed to be absent. In such circumstances, the reliability of the monitoring system becomes critically important. This reliability depends on statistical power, the ability of a method to detect real outcomes, often against a background of natural environmental variation, measurement error, and ignorance of biological processes.

Given the importance of reliable monitoring, the persistent failure of conservation biologists and ecologists to explicitly incorporate reliability considerations into the design of monitoring programs is notable (Fairweather 1991; Mapstone 1995). The task of stipulating an appropriate level of statistical power and an acceptable effect size is not simply a statistical decision. It entails judgments about the biological importance of an effect (Mapstone 1995). These judgments may be influenced, in part, by the social, political, and economic implications of the ensuing management or policy decisions. Such considerations are critically important because analysis indicates that without reliability calculations, experimenters often are overly optimistic about the reliability and representativeness of their samples. The risk of false optimism may be compounded by experimental designs that fail to account for the independence of replicates (Hulbert 1984).

These observations highlight a general failing in the interpretation of scientific data. The implications of this failing are especially important in conservation biology, where the consequences of wrong decisions may be irreversible (e.g., destruction of critical habitat or extinction of species). Thus, conservation biologists should seek to apply methods that minimize incorrect decisions. Such methods are readily accessible (Fairweather 1991; Thomas 1996) yet seldom applied.

One potential explanation for this lack of application suggests that different sorts of research may be needed if we are to improve the effectiveness of monitoring programs and the linkages between monitoring, decision making, conservation management, and policy. Research on human judgment under uncertainty suggests that humans have a widespread tendency to perceive patterns where none exist (Redelmeier and Tversky 1996). Efforts to

link monitoring programs to conservation decision making may need to explicitly consider such fundamental human psychological constraints.

Recently, there has been a chorus of calls for establishment of global monitoring of biodiversity trends. While well intentioned, such programs have the potential to waste time and use limited resources. Continued use and advocacy of unproven methods, regardless of scale, serve only to undermine the credibility of conservation biology as a legitimate scientific discipline, in academic, policy, and other public fora. More seriously, given the magnitude of current rates of human exploitation of biodiversity, a consensus is needed as to the priority questions monitoring should aim to answer. Once those questions have been identified, the development of credible, extensive, and selectively intensive monitoring is essential, to provide warnings and adequate opportunities to avoid biotic catastrophe (Beddington 1995).

Future Directions for Research

The examples provided here illustrate a few specific ways in which decision theory and monitoring can apply to conservation on the ground (Box 10.1). The application of decision theory to identifying solutions and evaluating alternatives is limited only by the imagination of conservation practitioners. Virtually every practical, real-world problem in nature conservation would benefit from application of a decision theory and adaptive management approach. Several aspects of decision theory as applied to conservation problems would benefit from further research to strengthen its potential as a practical tool for resource managers and conservation biologists. These include:

1. *Develop ways to assess social values and use them to define composite utilities to allow for the complex integration of ecology, social sciences, and economics in specific situations.* This has rarely been achieved, and most of the examples described here have dealt with simple biodiversity objectives, or multiple biodiversity objectives, while blithely ignoring the realities of real-world decision making. Multidisciplinary research in this area would be fruitful, yet the tradition of specialization within both the natural and the social sciences may mitigate against tackling these hard problems.
2. *Develop models that can tractably evaluate multiple biological and social objectives that are measured in different currencies (e.g., representation, probabilities of extinction, frequency and magnitude of disturbance events) and that may also interact with one another (e.g., cascading effects through food webs, differential influence of habitat fragmentation on population densities of species).* With such models, decision theory can be used to assess optimal strategies for achieving multiple objectives that collectively are considered to be integrated indices of, for example, ecological health or biological integrity. In this way, conservation

strategies can begin to move away from their tendency toward single-species management.

3. *Develop models that allow for assessment of the trade-offs involved for a wider, but more realistic, range of management options than what has been accomplished to date.* For example, with respect to the implementation of an ecological reserve system, such a set of realistic options might include acquiring a new reserve for the system, enlarging an existing reserve, or restoring an existing reserve to improve its quality. Moreover, the value of each of these management options may change depending on the timing of implementation. These same approaches could then be used to evaluate a wider range of management options for an existing reserve, independent of other reserves in the system, such as revegetation, species reintroduction, eradication of exotics, road closure, and restoration of disturbance regimes.
4. *Explicitly test a specific decision-theory model, in terms of whether the hypothetical optimal solution generally performs better than random, status quo, or no management.* This would be impossible for some objectives, like minimizing extinction probabilities. However, it would be possible for testing management activities that are repeated frequently in space and time, like weed management.
5. *Develop the tools that can tractably evaluate the relative sensitivity of the solutions to uncertainty in the true state of the system and the dynamics of the state variables.* This is important for giving resource managers insight about how robust predicted solutions are and where priorities should be placed for collecting additional data.
6. *Develop user interfaces that will allow resource managers to change models and quickly generate new solutions.* Those who use the models to generate solutions will rarely be the ones to develop the models in the first place, yet they need to be able to alter models to input new goals, new management options, new values for state variables, new descriptions of the dynamics among state variables, and new constraints. This happens not only because managers want to evaluate alternative scenarios and the robustness of solutions, but also because the political and economic realities of management never remain constant.
7. *Develop and test rules for the selection of surrogate and indicator species.* Since we can feasibly measure only a handful of environmental attributes, we urgently need a set of robust rules to help determine which attributes will be most informative.
8. *Develop and test rules of thumb for conservation practice and implementation of active adaptive management.* Conservation practitioners must make many decisions, and their resources for modeling, experimental design, and evaluation are limited. While it is important for conservation biology researchers to pro-

vide guidance on best practice in decision making and monitoring, we must also deliver robust rules of thumb that can be generically applied and improve the consequences of conservation management in the short term.

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LITERATURE CITED

- Alford, R.A., and S. Richards. 1999. Global amphibian declines: A problem in applied ecology. *Annual Review of Ecology and Systematics* 30: 133–165.
- Andelman, S.J., and W.F. Fagan. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences* 97:5954–5959.
- Andelman, S.J., and E. Meir. In press. Breadth is better than depth: Biodiversity requirements for adequate reserve networks. *Conservation Biology*.

BOX 10.1. Research Priorities for Conservation Biology in Decision Making and Monitoring

Summary priority: Develop and implement integrated programs of adaptive decision making and monitoring (active adaptive management):

1. Develop and test rules for the selection of surrogate indicator species.
- *2. Determine whether decisions based on meeting a single biodiversity objective meet the needs of other biodiversity objectives.
- *3. Develop and test rules of thumb for conservation practice.
4. Create usable composite objectives that incorporate social and economic values.
5. Improve the way uncertainty and risk are incorporated into decision making.
6. Determine what kinds of decision-making methods work.
- *7. Isolate gaps in data that impede performance evaluation for making decisions.
- *8. Determine factors impeding collaboration between managers and researchers.
9. Transform environmental policy (e.g., National Environment Policy Act) to trigger monitoring that enhances decision making.

Note: Asterisks indicate the most urgent priorities.

- Beddington, J. 1995. Fisheries—The primary requirements. *Nature* 374:213–214.
- Beenhakker, H.L. 1975. *Capital Investment Planning for Management and Engineering*. Rotterdam: Rotterdam University Press.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821–841.
- Blaustein, A., D. Wake, and W. Sousa. 1994. Amphibian declines: Judging stability, persistence and susceptibility of populations to local and global extinction. *Conservation Biology* 8: 60–71.
- Bradshaw, G.A., M.-J. Fortin, and H.C. Biggs. In review. Large-scale monitoring of terrestrial and aquatic systems: Matching what science can do with what society wants. *Conservation Biology*.
- Caro, T.M., and G. O'Doherty. 1999. On the use of surrogate species in conservation biology. *Conservation Biology* 13:805–814.
- Clemen, R.T. 1996. *Making Hard Decisions: An Introduction to Decision Analysis*. Pacific Grove, Calif.: Duxbury Press.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. *Ecological Applications* 8:309–322.
- Fairweather, P. G. 1991. Statistical design and power requirements for environmental monitoring. *Australian Journal of Marine and Freshwater Research* 42:555–567.
- Ferson, S., and M.A. Burgman. 2000. *Quantitative Methods for Conservation Biology*. New York: Springer-Verlag.
- Guikema, S., and M. Milke. 1999. Quantitative decision tools for conservation programme planning: Practice, theory and potential. *Environmental Conservation* 26:179–189.
- Hanski, I. 1999. *Metapopulation Ecology*. Oxford: Oxford University Press.
- Hulbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54:187–211.
- Intriligator, M. D. 1971. *Mathematical Optimisation and Economic Theory*. Englewood Cliffs, N.J.: Prentice-Hall.
- James, F.C., C.E. McCullough, and D.A. Wiedenfield. 1996. New approaches to the analysis of population trends in land birds. *Ecology* 77:13–27.
- Kareiva, P.K., S.J. Andelman, D. Doak, B. Eldred, M. Groom, J. Hoekstra, L. Hood, F. James, J. Lamoreux, G. LeBuhn, C. McCulloch, J. Regetz, L. Savage, M. Ruckelshaus, D. Skelly, H. Wilbur, K. Zamudio, and the NCEAS HCP Working Group. 1999. *Using Science in Habitat Conservation Plans*. Santa Barbara, Calif.: National Center for Geological Analysis and Synthesis; Washington, D.C.: American Institute of Biological Sciences.
- Kulkarni, R.B., R.L. Burns, J. Wright, B. Apper, T.O. Baily, and S.T. Noack. 1993. Decision analysis of alternative highway alignments. *Journal of Transportation Engineering* 119:317–332.
- Landres, P., J. Verner, and J. Thomas. 1988. *Conservation Biology* 2:316–328.
- Lubow, B. C. 1996. Optimal translocation strategies for enhancing stochastic metapopulation viability. *Ecological Applications* 6:1268–1280.

- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, N.J.: Princeton University Press.
- Maguire, L. A., U. S. Seal, and P. F. Brussard. 1987. Managing a critically endangered species: The Sumatran rhino as a case study. In *Viable Populations for Conservation*, ed. M. E. Soulé, pp. 141–158. Cambridge, U.K.: Cambridge University Press.
- Maguire, L.A., and C. Servheen. 1992. Integrating biological and social concerns in endangered species management: Augmentation of grizzly bear populations. *Conservation Biology* 6:426–434.
- Mapstone, B. D. 1995. Scalable decision rules for environmental impact studies—Effect size, type-I and type-II errors. *Ecological Applications* 5:401–410.
- Margules, C. R., and Pressey, R.L. 2000. Systematic conservation planning. *Nature* 405:243–253.
- Meffe, G.K., and C.R. Carroll. 1997. *Principles of Conservation Biology*, 2nd ed. Sunderland, Mass.: Sinauer Associates.
- Meir, E., and S. J. Andelman. In press. Biodiversity data requirements for adequate reserve system design. *Ecological Applications*.
- Mulder, B.S., B.R. Noon, C.J. Palmer (and others), tech. coords. 1999. *The Strategy and Design of the Effectiveness Monitoring Program for the Northwest Forest Plan*. General Technical Report, PNW-GTR. Washington, D.C.: USDA, Forest Service.
- Noon, B.R., and B.B. Bingham. In press. The northern spotted owl as an umbrella species for late seral forests of the Pacific Northwest. In *Single-Species Approaches to Ecosystem Conservation*, eds. P. Foster-Tukey, P. Kelly, and R. Medellin. Washington, D.C.: Island Press.
- Noon, B.R., T.A. Spies, and M.G. Raphael. 1999. Conceptual basis for designing an effectiveness monitoring program. In Mulder, B.S., B.R. Noon, C.J. Palmer (and others), tech. coords., *The Strategy and Design of the Effectiveness Monitoring Program for the Northwest Forest Plan*, pp. 17–39. General Technical Report, PNW-GTR. Washington, D.C.: USDA, Forest Service.
- NRC (National Research Council). 2000. *Ecological Indicators for the Nation*. Washington, D.C.: National Academy Press.
- Parma, A., P. Amarasekare, M. Mangel, J. Moore, W. W. Murdoch, E. Noonburg, M. A. Pascual, H. P. Possingham, K. Shea, W. Wilcox, and D. Yu. 1998. What can adaptive management do for our fish, food, forests and biodiversity? *Integrative Biology* 1:16–26.
- Possingham, H. P. 1997. State-dependent decision analysis for conservation biology. In *The Ecological Basis of Conservation: Heterogeneity, Ecosystems and Biodiversity*, eds. S.T.A. Pickett, R.S. Ostfeld, M. Shachak, and G.E. Likens, pp. 298–304. New York: Chapman and Hall.
- Possingham, H., and K. Shea. 1999. The business of biodiversity. *Australian Zoologist* 31:3–10.
- Possingham, H. P., I. R. Ball, and S. Andelman. 2000. Mathematical methods for reserve system design. In *Quantitative Methods for Conservation Biology*, eds. S. Ferson and M. Burgman, pp. 291–306. New York: Springer-Verlag.

- Pulliam, H.R. 1988. Source, sinks and population regulation. *American Naturalist* 132:652–661.
- Ralls, K., and J. Ballou. 1986. Captive breeding programs for populations with a small number of founders. *Trends in Ecology and Evolution* 1:19–22.
- Ravirala, V., and D.A. Grivas. 1995. Goal-programming methodology for integrating pavement and bridge programs. *Journal of Transportation Engineering* 121:345–351.
- Redelmeier D.A., and A. Tversky. 1996. On the belief that arthritis pain is related to the weather. *Proceedings of the National Academy of Science USA* 93:2895–2896.
- Richards, S.A., H.P. Possingham, and J. Tizard. 1999. Optimal fire management for maintaining community diversity. *Ecological Applications* 9:880–892.
- Shea, K., P. Amarasekare, M. Mangel, J. Moore, W. W. Murdoch, E. Noonburg, A. Parma, M. A. Pascual, H. P. Possingham, W. Wilcox, and D. Yu. 1998. Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution* 13:371–374.
- Simberloff, D. 1998. Flagships, umbrellas and keystones: Is single species management passé in the landscape era? *Biological Conservation* 83:247–257.
- Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. *Forest Ecology and Management* 115:101–111.
- Teng, J., and G. Tzeng. 1996. A multi-objective programming approach for selecting non-independent transportation investment alternatives. *Transportation Research* 30B:291–307.
- Thomas, L. 1996. Monitoring long-term population change: Why are there so many analysis methods? *Ecology* 77:49–58.
- Thompson, W.L., G.C. White, and C. Gowan. 1998. *Monitoring Vertebrate Populations*. New York: Academic Press.
- Williams, P.H., N.D. Burgess, and C. Rahbek. In press. Flagship species, ecological complementarity, and conserving the diversity of mammals and birds in sub-Saharan Africa. *Animal Conservation*.

ECOLOGICAL RESTORATION

A Key to Conservation Biology's Future

James A. MacMahon and Karen D. Holl

The success or failure of most restoration projects depends heavily on such ecological processes as demographic stochasticity, environmental stochasticity, intra- and interspecific interactions, habitat scale, and habitat destruction. Hence, restoration ecology should draw heavily from and contribute to these ecological principles. The question becomes one of identifying those areas of ecology that offer promise and deserve scrutiny within restoration ecology.

—J. S. Brown

Research in restoration ecology has grown exponentially in the past twelve years (Young 2000; Soulé and Kohm 1989). This growth is the result of increasing recognition that restoration is a necessary component of conservation, as much of the world is disturbed, and intact natural systems are disappearing. In contrast, abandoned and degraded lands are increasing and may become some of the only lands available for conservation. Moreover, as the opening quote from Brown identifies, besides producing a desired change in a system, attempts at restoration may also reveal insights into ecosystem functioning, and, therefore, may help in preventing or minimizing damage in the first place.

That said, we must reiterate at the outset a few oft-stated cautions regarding the potential for restoration. Although restoration may further conservation efforts, it is a second choice to preserving more intact habitats and should not serve as an alternative for preservation. Because restoration is difficult and often unsuccessful in restoring native ecosystem structure and functioning, restoration ecologists should stress the unparalleled value of preservation. Restoration will necessarily compete for funding with other conservation efforts, and it is important to carefully consider the best expenditure of funds to further conservation on a regional scale.

As Ehrenfeld (2000) notes, restoration efforts are motivated by a broad spectrum of reasons, ranging from permit compliance to reducing the threat of extinction of a single species to restoring ecosystem disturbance patterns across entire watersheds. To achieve restoration for conservation ends requires meeting lofty goals, such as restoring connectivity with the surrounding landscape, self-maintaining disturbance regimes such as flooding (Cairns and Heckman 1996), and a variety of hydroperiods that can influence community composition, such as amphibian species diversity (Snodgrass et al. 2000). Selecting the most appropriate goals for restoration can be highly controversial, and the task is particularly difficult because of the common lack of undisturbed reference systems or pre-impact data (Palmer et al. 1997). This book being focused on research priorities in conservation biology, our highest-priority research questions are those that must be answered so that restoration efforts can maximize the conservation of biodiversity.

We focus the discussion on the community and ecosystem levels of integration, despite the focus of much of conservation biology on the restoration of populations of particular species (Bowles and Whelan 1994; Montalvo et al. 1997; cf. Simberloff et al. 1999). We feel restoration efforts must necessarily aim to restore entire ecosystems, as it is difficult to restore species populations without restoring the abiotic environment conducive to a species persistence and reproduction and interactions with many other species; conversely, biotic communities strongly influence the abiotic environment. While there are some differences in applying restoration to terrestrial as opposed to aquatic systems (Mitsch et al. 1998), we fuse both in our discussion and highlight a few of the differences where appropriate. Because of the interdependence of terrestrial and aquatic ecosystems, their restoration should be integrated (NRC 1992); it is impossible to restore rivers, lakes, wetlands, or marine systems if material and energy fluxes from adjacent terrestrial systems are not restored to natural levels.

Multiple Faces of Restoration

To provide common ground and clarify goals, we briefly define several types of activity that fall under the general umbrella of restoration. Strictly speak-

ing, restoration means bringing an ecological system back to its original or former state (Bradshaw 1997). In the context of conservation biology, it is distinct from such actions as preservation, conservation, and stewardship. The common thread between restoration and these other activities is that they all involve efforts devised to overcome alterations caused by natural or anthropogenic forces.

The term *restoration* implies that the system's original state was good or perfect (Francis et al. 1979). In contrast, *rehabilitation* is an attempt to restore elements of a structure or functioning of an ecosystem without necessarily attempting complete restoration to a prior condition. *Reclamation* involves the rehabilitation of severely degraded sites. Generally, the result of this is not a return to a prior condition, but achievement of a condition where some stabilization of the degradation process occurs and inroads are made toward restoring certain species and ecosystem processes. *Re-creation* is an attempt at wholesale reconstruction of an ecosystem on sites so severely disturbed that there is little left to restore; the product may not represent the historical system. This is often a difficult activity, but it can yield important insights into ecological processes as one develops model ecosystems.

Finally, simply allowing a disturbed system to follow its natural trajectory is referred to as *ecological recovery* (succession). In many cases, ecological recovery is undesirable, particularly in terrestrial systems, because of the time involved and the uncertainty of the result; but it may be the de facto restoration strategy when resources are limited. Some aquatic systems, however, are sufficiently resilient that if stresses are removed, they recover fairly quickly (Cairns and Heckman 1996).

All of these processes of restoration typically require intensive management, and their success should be defined by an unambiguous statement of the goal of the process (MacMahon 1997; Michener 1997; White and Walker 1997). In this discussion we generally refer to restoration, rehabilitation, and reclamation under the general term *restoration*. Restoration per se will not be our sole focus, simply because it is extremely difficult, time consuming, and, therefore, expensive if done correctly (Jackson et al. 1995). Moreover, there is much more gray area among these three terms than most restoration ecologists acknowledge. Although it is important to define how restoration is used in specific case studies, lengthy semantic debates are not productive (Hobbs and Norton 1996; Ehrenfeld 2000). In this chapter, we do not strongly focus on *de novo* habitat creation, as extensive evidence suggests that substituting created habitat for existing habitat seldom furthers conservation efforts, although it provides insights into what extreme management actions we may be forced to employ in the future. We do discuss one form of habitat creation, designer ecosystems, but it is recommended only under special, extreme circumstances to conserve certain species.

Research Priorities in Restoration Ecology

Rather than outlining research priorities specific to certain ecosystem types, we suggest general areas of urgency, using examples from a range of ecosystems. We refer readers to two other recent efforts to prioritize research areas in restoration ecology. First, a workshop was held at the National Center of Ecological Analysis and Synthesis in Santa Barbara entitled "Research Priorities in Restoration Ecology" (Allen et al. 1997), the ideas from which are summarized in a special feature of *Restoration Ecology* (vol. 5, issue 4, 1997). In addition, the book *Restoration of Aquatic Ecosystems* (NRC 1992) outlines a number of research priorities for aquatic ecosystem restoration. We draw heavily on both these sources, although we have necessarily condensed their ideas and couched them in a conservation biology context.

We organize our research questions into five somewhat overlapping or related themes: the recovery process, using succession as a template for thinking about restoration; introduction of species; scale; evaluation of success; and policy. The latter topic requires collaborative research between natural and social scientists to successfully implement restoration. Those research questions that workshop participants agreed were of highest priority for restoration are listed in box 11.1. Below we provide a brief discussion of the underlying rationale for those questions.

Recovery Processes

Much research in restoration ecology has been focused on documenting observed patterns. Restoring ecosystems requires an understanding of the processes that lead to their development. Studies that have investigated the assembly rules governing the order of species entry into disturbed ecosystems suggest that there may be multiple potential endpoints for ecosystems (Hobbs and Norton 1996; Lockwood 1997). Understanding the factors that lead to different successional trajectories is essential to designing specific plans to restore areas.

Since succession is generally viewed as the natural recovery of altered ecological systems, logic dictates that we turn to succession, as first described by Clements (1916), to organize our initial thoughts about restoration (MacMahon 1998) and ask how our knowledge of succession might apply to the attainment of conservation goals. Succession begins with some disturbing event that is characterized by its areal extent, intensity, type, timing, and other attributes (White and Pickett 1985).

The most important aspect of the disturbance process is what is left afterward (residuals or legacies; cf. Franklin and MacMahon 2000), because those remaining components and organisms are the starting point for recovery. Following a disturbance, a variety of organisms and nonliving materials may

move ("migrate") or be moved to the site, depending on the migrants' distance from the disturbed site and their vagility. A low-vagility species is not likely to colonize the site, but one with high vagility could arrive in a matter of minutes to hours, if it was sufficiently nearby. Recently disturbed sites become a mix of residuals and migrants. Clements aptly pointed out that these organisms will not necessarily be part of the subsequent communities and ecosystems as they develop. Environmental conditions in the post-disturbance habitat edit out those migrants not suited for the site at that time, as well as those survivors whose world is so altered that their tolerance capacity is exceeded.

Understanding migration and establishment is an important facet of restoration, especially since species in restoration projects are usually rare species (Maina and Howe 2000), and dispersal from nearby areas can augment the recovery process. During restoration, we can act as agents of migration, and we can also create conditions to permit establishment. Thus, these two processes are among the most amenable to management. One difference between terrestrial and aquatic systems may be the rate of reintroduction of many species. Disturbed streams, because of the power and continuity of currents, may carry large objects, allowing recolonization to occur faster than on land, where air movement generally carries smaller loads and is less continuous. Organisms that live on land may require active migration more often than those in water that can be passively moved; however, lakes and ponds with few inlets may require migration processes more like those in terrestrial systems than those in flowing water.

Eventually, migrants and residuals establish a variety of interactions that act as a further filter in determining the species composition of the evolving community or ecosystem. For example, a predator or parasite that has the capacity to remove one of the migrants or residuals can change the community composition (Louda 1994). On the other hand, a species may be successful and capable of establishment only if it is associated with another species. Numerous mutualisms, such as pollination, seed dispersal, protection from herbivory, and mycorrhizal interactions, can have significant impact on an evolving community (Handel 1997). For example, the association of mycorrhizal fungi with plants can confer an advantage on both that allows them to remain a part of the developing community when individuals that do not develop a mutualistic relationship disappear (Allen 1991).

Once established, migrants and residuals alter the site, in the "reaction" process of Clements (1916). Such an altered site may develop characteristics that no longer favor some of the successful residuals or early migrants, and a new mixture of migrants may be favored. In many instances, some residuals are unable to withstand the early post-disturbance environment but persist in

the form of long-lived propagules that experience a suitable habitat after the process of reaction and are thus able to establish as a component of the developing system (Franklin et al. 1985). If the constantly changing environment and the consequent substitution of species come to a point of relative stability, the system appears, at least to our superficial perception, to remain unchanged. Obviously, we no longer believe that most systems show true stability; however, the sense of stability is occasioned by the persistence of long-lived woody perennials. A forest often does not change in gross appearance for decades or more, despite the fact that, other than a dozen tree species, all of its species populations turn over rapidly, changing the composition and the nature and magnitude of a variety of dynamic processes appreciably.

To alter the successional trajectory of a system to conserve certain species, it may be necessary to alter or direct one or more of those successional processes. Often this is done by speeding up succession, by preventing it from moving beyond a desired stage, or by introducing a species that might not colonize naturally. For example, lack of seed dispersal by animals is a major factor impeding the recovery of tropical forests in disturbed areas. Therefore, restoration efforts in such places have focused on planting trees and shrubs to attract animals, thus enhancing seed dispersal and accelerating succession (Holl and Kappelle 1999). Clearly, detailed knowledge of succession is necessary to restore communities and ecosystems to support conservation goals.

Assembly Rules

Since restoration is the reassembly of communities through human intervention, the search for rules in nature is of considerable importance to restoration ecologists. A recent perspective on ecological assembly rules (Weiher and Keddy 1999) shows the divergence of opinion as to whether rules actually exist. These range from the opinion that there has been a failure to demonstrate simple, general assembly rules to date, to the opinion that assembly rules, based on the assembly of guilds rather than species, are indeed robust and demonstrable in nature, confirming Diamond's (1975) suggestions. A search of the literature suggests that assembly rules probably do exist, but that there is sufficient variation among systems that they do not give exact predictions. Nonetheless, many attributes of developing systems predispose them to being invaded by a new species, including exotics, or to extinction of a resident species, thus causing compositional turnover. If we can quantify these attributes or determine likelihood of invasion and/or extinction events, we may be able to dramatically increase the efficiency of the restoration process. This is especially important to conservation goals if assembly rules are general, deterministic, and mechanistic (Belyea and Lan-

caster 1999), and such rules may even include attributes of the past history of a site (Kettle et al. 2001; Anderson et al. 2000).

In attempting to describe some aspects of ecological assembly, Keddy (1999) listed three principles that exhibit our understanding of the interplay of environmental factors and ecological patterns. First, any particular community or ecosystem is produced by multiple environmental factors acting simultaneously. Second, there are quantitative relationships between environmental factors and the properties of communities. Third, multiple factors that produce a community or ecosystem will change through time. If one examines these three, it is clear why we often have moving targets in the process of restoration and difficulty in its use as a valuable tool for conservation, either because of the time frame in which we operate, or because of the changing composition of species that are involved. One way to deal with some of these problems is to simplify communities through the use of guilds or functional groups. If this approach is applied with discretion and with the recognition that guilds are not necessarily natural entities, such an approach can lead to useful results during restoration (Hawkins and MacMahon 1989).

Structure and Function

Conservation biology has traditionally focused on conserving native species rather than preserving ecosystem processes. Likewise, the endpoint to the restoration process is often defined by the community composition rather than the establishment of normal processes. Although there is not always one-to-one correspondence between species composition and ecosystem processes (Zedler and Calloway 1999), it is clear that they are intricately related. Feedback loops between structure and function may help to maintain restored areas in certain states or may make restoration of degraded sites difficult. For example, Boyer and Zedler (1998) found that low nitrogen levels due to improper sediment texture in salt marshes in Southern California resulted in low cordgrass growth. Short cordgrass resulted in low populations of a native predatory coccinellid beetle that requires tall cordgrass during high tides. This resulted in an outbreak of a scale insect on the cordgrass that was normally controlled by the beetle. The failure to restore an appropriate sediment type led to an altered trajectory of recovery.

These feedback loops between structure and function are poorly understood, and research to elucidate these relationships is critically needed (Ehrenfeld and Toth 1997). In particular, little research has addressed the ability of soil and aquatic microbial communities to recover both composition and functional processes such as decomposition (discussed further in chapter 6). There has been a great deal of debate recently about the related question of whether some species are redundant from a functional standpoint (Tilman

et al. 1997; Hooper and Vitousek 1997). Recent studies (Nijs and Impens 2000) suggest that increasing the number of functionally analogous species enhances ecosystem reliability (probability of functioning), while increasing the number of functions these species support has a negative influence. These questions are particularly important in the context of deciding whether to try to restore all species (Palmer et al. 1997) or merely a functionally important subset of the total community.

Understanding the relationship between structure and function is important not only for conserving species but also for to gaining widespread public support for restoration. While conservation biologists generally support conservation of species for their inherent worth, if restored ecosystems can also provide processes critical to humans, such as flood control or nutrient uptake, it will be easier to obtain funding for such restoration.

Community Architecture

Many of our conservation activities, as well as restoration activities, emphasize the management of individual species by directly operating on their population characteristics or a variety of their species-specific requirements. It is not possible to find the funds to look at every species in a particular community or ecosystem. Rather than trying to manipulate individual species, we suggest that manipulating the architecture of the system may produce both the target ecosystem processes and patterns of ecosystem components in some cases. This means both the horizontal distribution of entities, often referred to as dispersion, and the vertical distribution of entities, frequently referred to as architecture or form. There are many examples in which architecture has been used to manage either species or communities. In native tallgrass prairie, the persistence of three-dimensional vegetation structure does not change over time, yet the species composition does. The stability of consumers relates to structure in these systems, not to species composition of the vegetation (Collins 2000). Simply thinning plants in agricultural or forestry contexts (changing the density and dispersion pattern) changes the composition of the fauna and flora of a particular area. While thinning directly affects processes such as competition, it also alters the structure of the system dramatically, and that structural change alone may be the direct cause of the organisms' responses. If we want more wood ducks, we generally put out more wood duck breeding boxes, under the assumption that this cavity nesting species is limited by the number of tree holes available and not by the food in an area. In aquatic systems the structure provided by downed woody debris is critical to invertebrates, fish, and the control of sediment movement (Harmon et al. 1986).

The idea of managing ecosystem components rather than species is hotly debated (Goldstein 1999; Walker 1999; Risser 1999). There should be little

question about whether architecture is important; rather, we need to know where and under what circumstances it is critical.

Our conservation efforts need to take into account the importance of system architecture. Under many scenarios, successful restoration of a system may depend as much on structure as it does on species composition. We need to know the extent of such relationships.

Interaction with Other Human-Induced Changes

Potential effects of climate change, elevated CO₂, and increased N availability on conservation goals are addressed in chapter 9. It is important to note, however, that all these factors are likely to affect the trajectory of succession and disproportionately affect disturbed ecosystems. For example, recently germinated seedlings are particularly susceptible to changes in precipitation (Woodward 1992; Larcher 1995), and increased N availability is likely to favor non-native species (Maron and Connors 1996). Likewise, interactions between species, such as nurse-plant effects (Ashton et al. 1997) and mycorrhizal associations (Egerton-Warburton and Allen 2000), may be altered by changes in climate and increased N availability. As we discuss later, most restoration work has focused on small scales and has not considered the effects of other human-induced change such as climate change, elevated CO₂, and increased nitrogen availability. Conversely, much of the research on the latter questions has focused on later-successional ecosystems. More research is needed that considers the interactions between other human-induced environmental changes and ecosystem recovery from disturbance. Such knowledge is important to the development of conservation plans. For example, if we propose to restore a certain species in its former range, but the conditions for establishment have been altered due to a change in climate, the plan will have little probability of success.

Introduction of Species

The introduction or reintroduction of species to disturbed sites raises a number of research questions that must be addressed to ensure that restoration results in net positive rather than negative effects on conservation.

Reintroduction of Species

Reintroduction of species to disturbed sites has a number of important consequences for the success of restoration and for maintenance of genetic integrity, thus having significant conservation implications (discussed in detail in Montalvo et al. 1997). First, a great deal of research has demonstrated that local adaptation to site conditions results in higher fitness (Bradshaw 1984; Huenneke 1991), suggesting that local adaptation is important to restoration success. But the spatial scale of local adaptation can range from

an order of meters for metal-tolerant plants (Antonovics and Bradshaw 1970) to many kilometers for plants adapted to a climatic gradient (Knapp and Rice 1998), and very little is known about this phenomenon. Second, introduction of nonlocal seed can have important consequences for the genetic integrity of surrounding populations (Montalvo et al. 1997). Managers are often forced to make decisions regarding the question of how local is local, which has important economic consequences given that seed collection is time consuming and expensive (Lippitt et al. 1994). Clearly, detailed studies of genetics will not be possible for all species, which means that research on the degree of local adaptation must be compiled to try to predict rules of thumb for scales of genetic variability based on life history and dispersal characteristics of species. For example, for *Elymus glaucus*, a primarily self-pollinating grass species with highly localized genetic differences, seed collection may need to be more spatially restricted than for conifer species that are wind pollinated and less genetically distinct (Knapp and Rice 1996). Questions of whether localized adaptation increases restoration success can be tested in restoration experiments (Montalvo et al. 1997).

Invasive Species

Invasive exotic species have an enormous effect on the establishment and survival of native species in disturbed areas, and their control is often the focus of restoration efforts (Berger 1993). Predicting invasions of exotic species and their potential to spread and have unwanted impacts is of particular importance to restoration given that disturbed areas are particularly susceptible to invasion (D'Antonio et al. 1999). Susceptibility to invasion may relate inversely to diversity (Levine 2000), but contrary to previous assertions, exotics invade areas of high native plant diversity (Stohlgren et al. 1999). This question is also important given that exotic species are sometimes introduced at early stages in restoration to ameliorate stressful conditions for later-successional species (Kuusipalo et al. 1995; Chapman and Chapman 1996). Therefore, guidelines are needed for when the use of exotics is appropriate depending on their potential impacts on other species. These research questions are addressed in more detail in chapter 4.

Designer Communities

More land is being altered at an ever increasing rate in the world than at any time in the past. This suggests that to "conserve" anything will require restoration at some level. The most damaged sites are often ignored for restoration projects because of the difficulty of restoring them to any semblance of a natural community. Even though regulations in many countries demand that restora-

tion be attempted, efforts are often unsuccessful because the goals set are unreasonable for the particular site. An alternative might be to design ecosystems that contain groups of species that do not generally exist together in nature but support some conservation goal. These "designer" ecosystems would be constructed of groups of species that are selected so that each has a specified purpose in a conservation plan. Many who review this idea presume that scientists are attempting to play God and dismiss it out of hand.

It seems reasonable, in severely disturbed sites, to ask the question, Can this site become more useful for the purposes of conservation if we create a unique assemblage of organisms? Such combinations may not persist on their own and may require constant management (Bridgewater 1988). We are painfully aware of the effect of introducing alien species. In the case of designer ecosystems, the optimal situation would be to combine species that are native in a general area, but usually do not occur together, to meet some goal. These need not even be different species; they could be different varieties or genotypes of the same species (Lesica and Allendorf 1999). In the extreme, however, if we knew enough about the biology of a particular group of species, we might put together a completely novel system whose components were drawn from around the world but whose characteristics had been studied so that the species could not cause problems elsewhere. Obviously, this is a difficult and risky venture that must be well studied and controlled from the outset. We would have to negate the environmental and economic costs of invaders (Pimentel et al. 2000) by predicting their invasiveness (Reichard and Hamilton 1997; Pysek 1998; Ruesink et al. 1995).

We often have a static view of communities as having a particular species composition. In fact, fossil data for both plants and animals suggest that many species do not associate now as they did in the past, and that community composition is highly changeable over time. The idea of forming communities of species that do not normally associate for some purpose has been around for a long time, and many successes have been obtained, even though the goal has not always been one of self-consciously developing a designer ecosystem. An example of considerable current interest to conservation biologists is the development of the traditional shade type of coffee plantations, in which layers of vegetation are fostered, as opposed to the open uni-layer of sun-grown coffee. The layers of traditional plantations contain native and non-native species, yet the structure mimics that of natural forests, and many animals and native plants form new combinations that did not typically occur (Greenberg et al. 1997). When the structure is altered to a form that is more open, the industrial non-shade coffee plantation, species diversity is lost (Perfecto et al. 1996; Roberts et al. 2000).

Scale

One of the most important questions in restoration ecology is how to prioritize restoration at larger scales. Funding for restoration as a conservation tool will always be limited, which means that managers will need to make decisions about where to restore (Clewett and Rieger 1997). Most restoration efforts have focused on small spatial and temporal scales (NRC 1996, 1997; Lockwood and Pimm 1999), the selection of sites often largely dictated by political and economic concerns rather than by ecological principles. The success of such restoration efforts in conserving species and ecosystems will depend on their position in the landscape relative to the condition, use, and community composition of land in the surrounding area (NRC 1992; Hobbs et al. 1993; Hansson et al. 1995). Restoring a natural trophic structure may require reintroducing large vertebrates, the movement of which is dictated by landscape patterns (Simberloff et al. 1999). Moreover, restoration of many disturbance-dependent ecosystems, such as ponderosa pine forests (Moore et al. 1999) and riparian systems (Sparks et al. 1998), requires managing disturbances at large scales. Also, ecological processes occurring at larger scales (e.g., dispersal) may affect local conservation and restoration efforts (Baillie et al. 2000).

Landscape Mosaic

The spatial arrangement of landscape elements influences ecosystem structure and functioning, and thus influences the attainment of conservation goals. A number of basic ideas from conservation biology and ecosystem ecology should help to inform restoration efforts directed to conservation goals. Davies et al. (chapter 5) list four ways in which the matrix surrounding a habitat fragment can affect population dynamics within the fragment; the surrounding habitat can: (1) alter dispersal and colonization rates, (2) provide habitat for focal species, (3) provide habitat for invasive species, and (4) affect biophysical processes. Restored areas can also have these interactions with the surrounding landscape matrix, although only recently have such ideas been applied in a restoration context. For example, Hobbs (1993) discusses options for allocating revegetation efforts. Revegetation buffers around existing patches may serve to ameliorate the microclimate in the existing patch, whereas restoring a corridor may provide connectivity between existing patches. Prioritizing areas to restore for specific animal species requires knowledge of their movement patterns. Based on measurements of movement patterns of the endangered Fender's blue butterfly (*Icaricia icarioides fenderi*), Schultz (1998) recommended restoring a series of stepping stone patches rather than a continuous corridor of habitat. Restoring wetlands requires restoring hydrological connectivity, as well as proxim-

ity to source populations of plants and animals. Although it has rarely been done, restoration provides an excellent opportunity to test ideas regarding the effect of the surrounding landscape experimentally (Hobbs 1993).

Patchiness and Disturbance

One of the greatest challenges of restoration is restoring the spatial and temporal variability of ecosystems. Many ecosystems are adapted to periodic disturbances that happen at a range of scales; for instance, grassland may be disturbed by rodent burrowing on an annual basis on the order of square centimeters and by fire on the scale of tens of years and many square kilometers. Some species even require disturbance in order to persist (Pavlovic 1994). The question arises as to whether there is a minimum size or time scale, for specific ecosystems, below which restoration efforts are futile (Ehrenfeld and Toth 1997). The massive Kissimmee River restoration project in Florida is aimed at 70 km of river channel and 11,000 ha of floodplain wetlands (Koebel 1995) and restoring the natural meandering of the river. Is restoring river processes at a smaller scale possible? Pink shrimp often use different areas of estuaries during different parts of the year, which requires restoring areas with a range of water depths to provide the temporal variability of habitats necessary (NRC 1994). Pickett and Thompson (1978) suggest that there is a "minimum dynamic area" that must be maintained to allow for a natural disturbance regime to provide sufficient source populations for recolonization, but such areas are rarely known for different species or ecosystem types (see also Baillie et al. 2000).

Quantitative Tools

Landscape-level processes take place at spatial and temporal scales that are not amenable to traditional methodologies of experimental design and inferential statistics. Studying restoration at large scales will require integration of information from smaller-scale experiments and ongoing restoration with modeling efforts. It will require the use of a range of quantitative techniques such as time series analysis, multivariate statistics, geostatistical approaches, simulation modeling of dispersal behavior, materials flux, and other spatial processes, and meta-analysis for unreplicated or nonexperimental data (Arnqvist and Wooster 1995; Michener 1997; Chapman 1999). More research is needed on the ability of different combinations of experimental and quantitative tools to predict system behavior at large scales. For example, Schultz and Crone (1998) used parameters estimated from small-scale burn plots to predict the outcome of different fire management strategies to restore habitat for the endangered Fender's blue butterfly. They also used sensitivity analysis to determine which parameters had the most influence on the model in order

to prioritize future data collection. In a special feature of *Restoration Ecology* (vol. 5, issue 4S, 1997), authors present various mapping techniques for prioritizing riparian restoration efforts that consider geomorphology (topography, channel properties, and sediment properties), hydrology, and existing vegetation. A similar approach has been used successfully for terrestrial landscapes (Palik et al. 2000). The accuracy of these approaches for predicting the outcome of restoration should be tested in actual restoration projects to determine their utility.

Evaluating Effectiveness of Restoration

Conservation planning and monitoring are discussed elsewhere in this volume (chapter 10), but monitoring is such a critical component of restoration that we feel it is important to highlight a couple of research questions. Setting clear goals for restoration is absolutely essential to select criteria on which to base progress and determine success (Hobbs and Norton 1996). For restoration to be successful as a conservation tool, progress toward clearly specified goals needs to be monitored and the results incorporated to modify subsequent restoration actions. Although there has been some research into developing criteria for monitoring restoration success (PERL 1990; Sutter 1996), much more work is needed in this area. Monitoring will need to be done at temporal and spatial scales sufficiently large to incorporate natural variability (discussed above; NRC 1992; White and Walker 1997).

It is important to evaluate the success of a restoration project, although this is not always done. Lockwood and Pimm (1999) examined eighty-seven restoration projects that met a number of criteria they considered to be important with regard to meeting the stated goals of the individual project, e.g., sustaining habitat, restoring productivity, and controlling erosion. In their study, using their personal interpretation of the goals of the projects, seventeen (20 percent) of the projects satisfied all the prescribed goals. An additional seventeen projects were generally completed unsuccessfully, leaving 60 percent of the projects judged to be partially successful. Lockwood and Pimm found that 97 of 184 (52 percent) specific goals were achieved. Sixty-one percent of the 80 functional goals and 104 structural goals were considered achieved. Although there are limitations to this review, it seems clear that the success rate is good enough that we should incorporate restoration into our conservation planning. We must emphasize, however, that not all of the goals listed by the practitioners in these examples are goals that would be appropriate for conservation biology, and some of conservation biology's goals might be more difficult to achieve.

An important aspect of the Lockwood and Pimm study is their finding that 48 percent of restoration projects stopped monitoring before achieving

stated goals, suggesting that most monitoring programs are conducted for too short a time. Given the common funding constraints on monitoring (Clewett and Rieger 1997), it is essential to carefully select variables or indicators that allow evaluation of the stated goals for a particular project.

Policy

Cairns and Heckman (1996) note that restoration ecology "is a bridge between the social and natural sciences." Although this volume focuses on biological research questions for conservation, it is impossible to separate biology and policy questions in restoration ecology. Prioritizing and researching these questions will necessarily require interdisciplinary research between natural scientists (biologists, chemists, hydrologists) and social scientists (political scientists, economists, sociologists). We list a few important topics.

Paying for Restoration

Although our ecological knowledge base for restoration is generally weak, the primary factor limiting restoration efforts is typically funding (Holl and Howarth 2000). Implementing research on restoration will require collaboration with economists and political scientists to develop creative ways for implementing restoration. One such example is the Partners for Fish and Wildlife Program of the U.S. Fish and Wildlife Service, which provides matching funds for landowners who voluntarily undertake restoration projects on their land (USFWS 1999). Likewise, in Costa Rica landowners are given tax breaks for reforesting logged land with native tree species (Butterfield and Fisher 1994). For each conservation project, it is important to determine what the most appropriate sources of funding should be.

Legislation

Legislation is an important control on restoration and conservation efforts, but often it is not designed to accommodate the dynamic nature of ecosystems. The difference in ecological and political time scales presents a major obstacle to legislating and financing restoration (NRC 1992). Usually, the success of restoration is judged after a relatively short time compared to that of natural ecosystem recovery. For example, success of mine reclamation in eastern hardwood forests is commonly judged after five years (Holl and Cairns 1994), a much shorter time than is necessary for recovery from natural disturbance. Moreover, the aggressive, non-native, herbaceous species commonly planted to achieve five-year cover requirements have been shown to inhibit the long-term development of the vegetational communities (Brenner et al. 1984; Burger and Torbert 1990; Holl, unpublished data). More work is

BOX 11.1. Research Priorities in Restoration

Questions are organized into categories paralleling the discussion.

Investigate Recovery Processes

1. What are the rate-limiting steps to recovery in different biomes?
2. To what degree does the species pool of early-establishing species affect the trajectory of recovery during restoration?
3. Does the sequence in which species are introduced to human-disturbed sites affect the successional trajectory or the speed of recovery?
4. To what degree does establishing appropriate abiotic conditions result in the establishment of the complement of native species? For example, since it would be impossible to reintroduce all soil microorganisms, does restoration of appropriate soil texture, nutrients, and temperature result in the reestablishment of the majority of species?
5. To what degree do we need to restore ecosystem processes such as nutrient cycling and water fluxes to restore native species and vice versa?
6. To what degree does the physical architecture of a community's components determine its species composition?
- *7. How is the trajectory of succession during restoration affected by other human-induced changes, such as climate change, elevated CO₂, and increased N availability? For example, will altered precipitation patterns favor the establishment of seedlings of non-native species in restored areas, thereby reducing the potential for recovery of native species?

Analyze and Synthesize the Results of Species Introductions

1. What are the effects of introduction of genotypes on restoration success and surrounding populations?
2. Are there rules of thumb for maintaining local adaptations?
3. What is the influence of numbers of individuals and genetic variation of the founding population on the success of reestablishing native species?

needed on how to develop mechanisms that recognize and respond to the inherent uncertainty involved in restoration, such as some form of "restoration insurance" if restoration efforts initially appear to be unsuccessful (Holl and Howarth 2000).

Regional Planning

Given the limited funding available and the ecological consequences of piecemeal restoration, work is needed on how to better coordinate restora-

4. Can we predict the invasion probability of species from easily defined traits?
5. Can we create "designer ecosystems" composed of species that normally do not co-occur that allow us to address specific conservation goals yet do not, themselves, impose threats (e.g., the escape of non-native species)?

Consider Spatial scale

- *1. How does the surrounding land-use matrix affect movement of organisms and materials into and population dynamics in restored areas and vice versa? For example, could restored areas serve as sink populations? Or, can restoration of habitat surrounding protected areas help to minimize edge effects within the protected area?
2. At what scale do we need to manage for natural temporal and spatial variability in restoration? Can we develop rules of thumb for minimum sizes of areas to restore for certain types of disturbance regimes or species?
3. What combination of tools (e.g., small-scale experiments, large-scale experiments, models) are useful in predicting success of restoring species at larger scales?

Implement and Analyze Monitoring

1. Which parameters should be selected for monitoring?
- *2. To what degree do early indications of restoration success suggest long-term establishment of native species?

Consider Policy Questions

1. What funding tools are most appropriate to ensure long-term success of restoration?
2. How can legislation be designed to better accommodate the dynamic nature of ecological systems?
3. What strategies could be used to coordinate policies and legislation to aim for regional restoration plans?

Note: Those priorities marked with an asterisk are those we consider to be most important.

tion at a regional scale. For example, the Coastal Wetlands Planning, Protection and Restoration Act calls for a planning group composed of local, state, and federal government agencies; private groups; scientists; and the public (Good 1993). Each year the planning group prioritizes project proposals based on their ecological importance and cost effectiveness; the proposed projects are reviewed at public hearings and ultimately approved by the state legislature and by Congress. Although the number of regional planning efforts is increasing, numerous private and public agencies involved in

restoration are still not coordinating efforts. Such coordination is particularly important in marine ecosystems, where reducing stresses to allow for ecosystem recovery necessarily means crossing numerous jurisdictional boundaries (NRC 1997).

Closing Thoughts

In 1987 Bradshaw wrote that “the successful restoration of a disturbed ecosystem is the acid test of our understanding of that system.” We have made progress in the field of restoration in designing experiments to better understand controls over ecosystem structure and function (Young 2000). That understanding leads to more effective conservation techniques and strategies. Yet restoration ecology has not realized its full potential to further our knowledge of ecological processes and dynamics and consequently to contribute to conservation initiatives. As mentioned throughout this chapter, restoration ecology provides the potential to do large-scale replicated experiments, but such experiments are surprisingly few. Much basic ecological theory, such as metapopulation dynamics and the ecology of exotic invaders (chapter 4; Simberloff et al. 1999), is not widely applied in restoration, despite its effective use in conservation.

Our experience and that of others (Allen et al. 1997) suggest that one of the main issues leading to the gap between theory and practice is the separation between people who are doing research and those who are implementing restoration projects. Many government agencies and nonprofit organizations fund implementation of restoration projects with a minimal research component, even though these agencies need the research to inform their management actions. Likewise, government science-funding agencies often support research on basic principles that underlie restoration, or that could be applied to restoration, but are unlikely to provide funding to work at the scale at which many restoration projects are implemented. We suggest that partnerships between research universities and public and private land management agencies be encouraged or in some cases required. This would give researchers incentive to work on “real-world” questions and management agencies incentive to design their restoration efforts in a manner to test specific hypotheses. For example, the U.S. National Park Service, which has traditionally been in the business of promoting tourism, is increasingly working to facilitate research in national parks (NPS 2000; M. Soukup, personal communication). Building such partnerships is critical to answering many of the questions outlined above and to ensuring the long-term success of conservation efforts globally.

We hope it is clear that developments in conservation biology and restoration ecology are interdependent in this rapidly changing world. Each field of

study requires and gains from intellectual movement in the other. Together they provide data and approaches that are directed to some of humankind's most challenging problems in both natural and managed systems (Daily 1995). Human needs and the ecological goals of restoration have a positive, reciprocal relationship (Geist and Galatowitsch 1999).

Finally, from our discussion, it is clear that much research is required for us to develop restoration strategies that support conservation efforts. Interestingly, such studies also add to the corpus of knowledge about the characteristics and rules that govern natural systems and should inform our efforts to conserve biodiversity in more intact ecosystems.

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LITERATURE CITED

- Allen, E.B., W.W. Covington, and D.A. Falk. 1997. Developing the conceptual basis for restoration ecology. *Restoration Ecology* 5:275–276.
- Allen, M.F. 1991. *The Ecology of Mycorrhizae*. Cambridge: Cambridge University Press.
- Anderson, R.C., J.E. Schwegman, and M.R. Anderson. 2000. Micro-scale restoration: A 25-year history of a southern Illinois barrens. *Restoration Ecology* 8:296–306.
- Antonovics, J., and A.D. Bradshaw. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity* 25:349–362.
- Arnqvist, G., and D. Wooster. 1995. Meta-analysis: Synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution* 10:236–240.
- Ashton, P.M.S., S. Gamage, I.A.U.N. Gunatilleke, and C.V.S. Gunatilleke. 1997. Restoration of a Sri Lankan rainforest: Using Caribbean pine *Pinus caribaea* as a nurse for establishing late-successional tree species. *Journal of Applied Ecology* 34:915–925.
- Baillie, S.R., W.J. Sutherland, S.N. Freeman, R.D. Gregory, and E. Paradis. 2000. Consequences of large-scale processes for the conservation of bird populations. *Journal of Applied Ecology* 37 (Suppl. 1):88–102.
- Belyea, L.R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402–416.
- Berger, J.J. 1993. Ecological restoration and nonindigenous plant species: A review. *Restoration Ecology* 1:74–82.
- Bowles, M.L., and C.J. Whelan (eds.). 1994. *Restoration of Endangered Species*. Cambridge: Cambridge University Press.
- Boyer, K.E., and J.B. Zedler. 1998. Effects of nitrogen additions on the vertical structure of a constructed cordgrass marsh. *Ecological Applications* 8:692–705.

- Bradshaw, A.D. 1984. Ecological significance of genetic variation between populations. In R. Dirzo, and J. Sarukhan (eds.), *Perspectives on Plant Population Ecology*, pp. 213–228. Sunderland, Mass.: Sinauer Associates.
- Bradshaw, A.D. 1987. Restoration: An acid test for ecology. In W.R.I. Jordan, M. Gilpin, and J.D. Aber (eds.), *Restoration Ecology*, pp. 23–29. Cambridge: Cambridge University Press.
- Bradshaw, A.D. 1997. What do we mean by restoration? In K.M. Urbanska, N.R. Webb, and P.J. Edwards (eds.), *Restoration Ecology and Sustainable Development*, chapter 2, pp. 8–14. Cambridge: Cambridge University Press.
- Brenner, F.J., M. Werner, and J. Pike. 1984. Ecosystem development and natural succession in surface coal mine reclamation. *Minerals and Environment* 6:10–22.
- Bridgewater, P.B. 1988. Synthetic plant communities: Problems in definition and management. *Flora* 180:139–144.
- Brown, J.S. 1994. Restoration ecology: Living with the prime directive. In M.L. Bowles and C.J. Whelan (eds.), *Restoration of Endangered Species*, pp. 355–380. Cambridge: Cambridge University Press.
- Burger, J.A., and J.L. Torbert. 1990. Mined land reclamation for wood production in the Appalachian region. In J. Skousen, J. Sencindiver, and D. Samuel (eds.), *Proceedings of the 1990 Mining and Reclamation Conference and Exhibition*, vol. 1, pp. 159–163. Morgantown, W.V.: West Virginia University.
- Butterfield, R.P., and R.F. Fisher. 1994. Untapped potential for native species reforestation. *Journal of Forestry* 92:37–40.
- Cairns J. Jr., 1989. Restoring damaged ecosystems: Is predisturbance condition a viable option? *Environmental Professional* 11:152–159.
- Cairns Jr., J., and J.R. Heckman. 1996. Restoration ecology: The state of an emerging field. In R.H. Socolow (ed.), *Annual Review of Energy and the Environment*, vol. 21, pp. 167–187.
- Chapman, C.A., and L.J. Chapman. 1996. Exotic tree plantations and the regeneration of natural forests in Kibale National Park, Uganda. *Biological Conservation* 76:253–257.
- Chapman, M.G. 1999. Improving sampling designs for measuring restoration in aquatic habitats. *Journal of Aquatic Ecosystem Stress and Recovery* 6:235–251.
- Clements, F.E. 1916. *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution of Washington, Publication Number 242, 1–512.
- Clewell, A., and J.P. Rieger. 1997. What practitioners need from restoration ecologists. *Restoration Ecology* 5:350–354.
- Collins, S.L. 2000. Disturbance frequency and community stability in native tall-grass prairie. *American Naturalist* 155:311–325.
- Daily, G.C. 1995. Restoring value to the world's degraded lands. *Science* 269:350–354.
- D'Antonio, C.M., T.L. Dudley, and M. Mack. 1999. Disturbance and biological invasions: Direct effects and feedbacks. In L. Walker (ed.), *Ecosystems of Disturbed Ground*, pp. 413–452. New York: Elsevier.
- Diamond, J.M. 1975. Assembly of species communities. In M.L. Cody and J.M. Diamond (eds.), *Ecology and Evolution of Communities*, pp. 342–444. Cambridge, Mass.: Harvard University Press.

- Egerton-Warburton, L.M., and E.B. Allen. 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10:484–496.
- Ehrenfeld, J.G. 2000. Defining the limits of restoration: The need for realistic goals. *Restoration Ecology* 8:2–9.
- Ehrenfeld, J.G., and L.A. Toth. 1997. Restoration ecology and the ecosystem perspective. *Restoration Ecology* 5:307–317.
- Francis, G.R., J.J. Magnuson, H.A. Regier, and D.R. Talhelm. 1979. *Rehabilitating Great Lakes Ecosystems*. Ann Arbor, Mich.: Great Lakes Fishery Commission.
- Franklin, J.F., and J.A. MacMahon. 2000. Perspectives. *Science* 288:1183–1185.
- Franklin, J.F., J.A. MacMahon, F.J. Swanson, and J.R. Sedell. 1985. Ecosystem responses to the eruption of Mount St. Helens. *National Geographic Research* 1:198–216.
- Geist, C., and S.M. Galatowitsch. 1999. Reciprocal model for meeting ecological and human needs in restoration projects. *Conservation Biology* 13:970–979.
- Goldstein, P.Z. 1999. Functional ecosystems and biodiversity buzzwords. *Conservation Biology* 13:247–255.
- Good, B. 1993. Louisiana's wetlands. *Restoration and Management Notes* 11:125–133.
- Greenberg, R., P. Bichier, A.C. Angon, and R. Reitsma. 1997. Bird populations in shade and sun coffee plantations in central Guatemala. *Conservation Biology* 11:448–459.
- Handel, S.N. 1997. The role of plant-animal mutualisms in the design and restoration of natural communities. In K.M. Urbanska, N.R. Webb, and P.J. Edwards (eds.), *Restoration Ecology and Sustainable Development*, chapter 7, pp. 111–132. Cambridge: Cambridge University Press.
- Hansson, L., L. Fahrig, and G. Merriam. 1995. *Mosaic Landscapes and Ecological Processes*. New York: Chapman and Hall.
- Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Auman, J.R. Sedell, G.W. Lienkaemper, K. Cromack Jr., and K.W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.
- Hawkins, C.P., and J.A. MacMahon. 1989. Guilds: The multiple meanings of a concept. *Annual Review of Entomology* 34:423–451.
- Hobbs, R.J. 1993. Can revegetation assist in the conservation of biodiversity in agricultural areas? *Pacific Conservation Biology* 1:29–38.
- Hobbs, R.J., and D.A. Norton. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4:93–110.
- Hobbs, R.J., D.A. Saunders, and G. Arnold. 1993. Integrated landscape ecology: A western Australian perspective. *Biological Conservation* 64:231–238.
- Holl, K.D. 1996. Restoration ecology: Some new perspectives. In A. Noble and R. Noble (eds.), *Preservation of Natural Diversity in Transboundary Protected Areas: Research Needs/Management Options*, pp. 25–35. Washington, D.C.: National Research Council.
- Holl, K.D., and J. Cairns Jr. 1994. Vegetational community development on reclaimed coal surface mines in Virginia. *Bulletin of the Torrey Botanical Club* 121:327–337.

- Holl, K.D., and R.B. Howarth. 2000. Paying for restoration. *Restoration Ecology* 8:260–267.
- Holl, K.D., and M. Kappelle. 1999. Tropical forest recovery and restoration. *Trends in Ecology and Evolution* 14:378–379.
- Hooper, D.U., and P.M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- Huenneke, L.F. 1991. Ecological implications of genetic variation in plant populations. In D.A. Falk and K.E. Holsinger (eds.), *Genetics and Conservation of Rare Plants*, pp. 31–44. New York: Oxford University Press.
- Jackson, L.L., N. Lopoukhine, and D. Hillyard. 1995. Ecological restoration: A definition and options. *Restoration Ecology* 3:71–75.
- Keddy, P. 1999. Epilogue: From global exploration to community assembly. In E. Weiher and P. Keddy (eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats*, pp. 393–402. Cambridge: Cambridge University Press.
- Kettle, W.D., P.M. Rich, K. Kindscher, G.L. Pittman, and P. Fu. 2000. Land-use history in ecosystem restoration: A 40-year study in the prairie-forest ecotone. *Restoration Ecology* 8:307–317.
- Knapp, E.E., and K.J. Rice. 1996. Genetic structure and gene flow in *Elymus glaucus* (blue wildrye): Implications for native grassland restoration. *Restoration Ecology* 4:1–10.
- Knapp, E.E., and K.J. Rice. 1998. Comparison of isozymes and quantitative traits for evaluating patterns of genetic variation of purple needlegrass (*Nassella pulchra*). *Conservation Biology* 12:1031–1041.
- Koebel Jr., J.W. 1995. An historical perspective on the Kissimmee River Project. *Restoration Ecology* 3:149–159.
- Kuusipalo, J., G. Adjers, Y. Jafarsidik, A. Otsamo, K. Tuomela, and R. Vuokko. 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: Understorey development in forest plantations. *Journal of Vegetation Science* 6:205–210.
- Larcher, W. 1995. *Physiological Plant Ecology*. New York: Springer-Verlag.
- Lesica, P., and F.W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: Mix or match? *Restoration Ecology* 7:42–50.
- Levine, J.M. 2000. Species diversity and biological invasions: Relating local process to community pattern. *Science* 288:852–854.
- Lippitt, L., M.W. Fidelibus, and D.A. Bainbridge. 1994. Native seed collection, processing, and storage for revegetation projects in the western United States. *Restoration Ecology* 2:120–131.
- Lockwood, J.L. 1997. An alternative to succession. *Restoration and Management Notes* 15:45–50.
- Lockwood, J.L., and S.L. Pimm. 1999. When does restoration succeed? In E. Weiher and P. Keddy (eds.), *Ecological Assembly Rules: Perspectives, Advances, Retreats*, pp. 363–392. Cambridge: Cambridge University Press.
- Louda, S.M. 1994. Experimental evidence for insect impact on populations of short-lived, perennial plants, and its application in restoration ecology. In M.L. Bowles

- and C.J. Whelan (eds.), *Restoration of Endangered Species*, pp. 118–138. Cambridge: Cambridge University Press.
- MacMahon, J.A. 1997. Ecological restoration. In G.K. Meffe and C.R. Carroll (eds.), *Principles of Conservation Biology*, 2nd ed., chapter 14, pp. 479–511. Sunderland, Mass.: Sinauer Associates.
- MacMahon, J.A. 1998. Empirical and theoretical ecology as a basis for restoration: An ecological success story. In M. Pace and P. Groffman (eds.), *Successes, Limitations, and Frontiers in Ecosystem Science*, pp. 220–246. New York: Springer-Verlag.
- Maina, G.G., and H.F. Howe. 2000. Inherent rarity in community restoration. *Conservation Biology* 14:1335–1340.
- Maron, J.L., and P.G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302–312.
- Michener, W.K. 1997. Quantitatively evaluating restoration experiments: Research design, statistical analysis, and data management considerations. *Restoration Ecology* 5:324–337.
- Mitsch, W.J., X. Wu, R.W. Nairn, P.E. Weihe, N. Wang, R. Deal, and C.E. Boucher. 1998. Creating and restoring wetlands: A whole-ecosystem experiment in self-design. *BioScience* 48:1019–1030.
- Montalvo, A.M., S.L. Williams, K.J. Rice, S.L. Buchmann, C. Cory, S.N. Handel, G.P. Nabhan, R. Primack, and R.H. Robichaux. 1997. Restoration biology: A population biology perspective. *Restoration Ecology* 5:277–290.
- Moore, M.M., W.W. Covington, and P.Z. Fule. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. *Ecological Applications* 9:1266–1277.
- Nijs, I., and I. Impens. 2000. Biological diversity and probability of local extinction of ecosystems. *Functional Ecology* 14:46–54.
- NPS (National Park Service). 2000. *Cooperative ecosystem studies units*. <http://www.cesu.org/cesu/introduction/brochure.html>. Accessed April 5, 2000.
- NRC (National Research Council). 1992. *Restoration of Aquatic Ecosystems*. Washington, D.C.: National Academy Press.
- NRC (National Research Council). 1994. *Restoring and Protecting Marine Habitat*. Washington, D.C.: National Academy Press.
- NRC (National Research Council). 1997. *Striking a Balance: Improving Stewardship of Marine Areas*. Washington, D.C.: National Academy Press.
- Pacific Estuarine Research Laboratory (PERL). 1990. *A Manual for Assessing Restored and Natural Coastal Wetlands with Examples from Southern California*. California Sea Grant Report No. T-CSVCP-021, La Jolla, California.
- Palik, B.J., P.C. Goebel, L.K. Kirkman, and L. West. 2000. Using landscape hierarchies to guide restoration of disturbed ecosystems. *Ecological Applications* 10:189–202.
- Palmer, M.A., R.F. Ambrose, and N.L. Poff. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5:291–300.
- Parker, V.T., and S.T.A. Pickett. 1997. Restoration as an ecosystem process: Implications of the modern ecological paradigm. In K.M. Urbanska, N.R. Webb, and

- P.J. Edwards (eds.), *Restoration Ecology and Sustainable Development*, chapter 3, pp. 17–32. Cambridge: Cambridge University Press.
- Pavlovic, N.B. 1994. Disturbance-dependent persistence of rare plants: Anthropogenic impacts and restoration implications. In M.L. Bowles and C.J. Whelan (eds.), *Restoration of Endangered Species*, pp. 159–193. Cambridge: Cambridge University Press.
- Perfecto, I., R.A. Rice, R. Greenberg, and M.E. Van der Voort. 1996. Shade coffee: A disappearing refuge for biodiversity. *BioScience* 46:598–608.
- Pickett, S.T.A., and J.N. Thompson. 1978. Patch dynamics and the design of nature reserves. *Biological Conservation* 13:27–37.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50:53–65.
- Pysek, P. 1998. Is there a taxonomic pattern to plant invasions? *Oikos* 82:282–294.
- Reichard, S.H., and C.W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* 11:193–203.
- Risser, P.G. 1999. Examining relationships between ecosystem function and biodiversity: Reply to Goldstein. *Conservation Biology* 13:438–439.
- Roberts, D.L., R.J. Cooper, and L.J. Petit. 2000. Use of premontane moist forest and shade coffee agroecosystems by army ants in western Panama. *Conservation Biology* 14:192–199.
- Ruesink, J.L., I.M. Parker, M.J. Groom, and P.M. Kareiva. 1995. Reducing the risks of nonindigenous species introductions. *BioScience* 45:465–477.
- Schultz, C.B. 1998. Dispersal behavior and its implications for reserve design in a rare Oregon butterfly. *Conservation Biology* 12:284–292.
- Schultz, C.B., and E.E. Crone. 1998. Burning prairie to restore butterfly habitat: A modeling approach to management tradeoffs for the Fender's blue. *Restoration Ecology* 6:244–252.
- Simberloff, D.J., D. Doak, M. Groom, S. Trombulak, A. Dobson, S. Gatewood, M.E. Soulé, M. Gilpin, C. Martinez del Rio, and L. Mills. 1999. Regional and continental restoration. In M.E. Soulé and J. Terborgh (eds.), *Continental Conservation: Scientific Foundations of Regional Reserve Networks*, pp. 65–98. Washington, D.C.: Island Press.
- Snodgrass, J.W., M.J. Komoroski, A.L. Bryan Jr., and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: Implications for wetland regulations. *Conservation Biology* 14:414–419.
- Soulé, M.E., and K.A. Kohm. 1989. *Research Priorities in Conservation Biology*. Washington, D.C.: Island Press.
- Sparks, R.E., J.C. Nelson, and Y. Yin. 1998. Naturalization of the flood regime in regulated rivers. *BioScience* 48:706–720.
- Stohlgren, T.J., D. Binkley, G.W. Chong, M.A. Kalkhan, L.D. Schell, K.A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25–46.
- Sutter, R.D. 1996. Monitoring. In D.A. Falk, C.I. Millan, and M. Olwell (eds.), *Restoring Diversity: Strategies for Reintroduction of Endangered Plants*, pp. 235–264. Washington, D.C.: Island Press.

- Tilman, D., J. Knops, D. Wedin, P. Reich, M. Ritchie, and E. Siemann. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277:1300–1302.
- USFWS (United States Fish and Wildlife Service). 1999. *Partners for Fish and Wildlife Program: Cumulative Accomplishments*. <http://www.fws.gov/r9dhcpfw/ACCOMPS/Accomps.htm>. Accessed March 11, 1999.
- Walker, B. 1999. The ecosystem approach to conservation: Reply to Goldstein. *Conservation Biology* 13:436–437.
- Weiher, E., and P. Keddy (eds.). 1999. *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge: Cambridge University Press.
- White, P.S., and S.T.A. Pickett. 1985. Natural disturbance and patch dynamics: An introduction. In S.T.A. Pickett and P.S. White (eds.), *The Ecology of Natural Disturbance and Patch Dynamics*, pp. 3–13. New York: Academic Press.
- White, P.S., and J.L. Walker. 1997. Approximating nature's variation: Selecting and using reference information in restoration ecology. *Restoration Ecology* 5:338–349.
- Woodward, F.I. 1992. A review of the effects of climate on vegetation: Ranges, competition, and composition. In R.L. Peters and T.E. Lovejoy (eds.), *Global Warming and Biological Diversity*, pp. 105–123. New Haven, Conn.: Yale University Press.
- Young, T.P. 2000. Restoration ecology and conservation biology. *Biological Conservation* 92:73–83.
- Zedler, J.B., and J.C. Callaway. 1999. Tracking wetland restoration: Do mitigation sites follow desired trajectories? *Restoration Ecology* 7:69–73.

CONSERVATION BIOLOGY RESEARCH

Its Challenges and Contexts

Michael E. Soulé and Gordon H. Orians

Eighty percent of success is showing up.

—Woody Allen

What is conservation biology for? The conventional answer to that question has been that its purpose is to provide guidance to conservationists, so that they can do their work of protecting nature armed with the best available tools and knowledge. That answer reflects the belief that the main task of conservationists is to design, construct, and manage protected areas, a belief based on the correct perception that conservation of nature requires whole ecological systems, with their dynamic, changing, complex interactions over space and through time.

Reserves have two main functions in a conservation strategy. First, they can represent and house the biodiversity of a region. Second, they can shield the biodiversity they contain from processes that may threaten its persistence. However, reserves can fulfill these roles only if they contain a relatively complete, unbiased sample of a region's biodiversity and if they are large enough to protect their contained biodiversity from external threats.

Unfortunately, existing reserves contain a highly biased sample of Earth's ecosystems (Margules and Pressey 2000). For example, most of the areas that are protected in the United States have poor soils or low rainfall or are high-elevation terrain covered by rock and ice (Scott et al. 2000). In other words, the least valuable and productive areas have been favored for protection. Similarly, many marine protected zones have been established in areas with little commercial value, either because they were originally areas of low productivity or because they had already been fished out. Also, there are too few reserves and they are too small (see the preface). Important efforts are underway to correct for these deficiencies, but they are likely to achieve only partial success.

Therefore, although protected areas are the essential core of conservation strategies, by themselves they are not sufficient for the task of preserving nature. Some have argued that we also need to change the ways we use lands and waters that are not given protected status, the so-called matrix lands, which must play a more important role in conservation than they have heretofore. Unfortunately, the intensification of economic uses of nonprotected lands is steadily decreasing their value for nature protection and their use as buffer zones (Groom et al. 1999). Other components of the conservation toolbox, such as *ex situ* conservation facilities (zoos, aquariums, botanic gardens), have value, but their overall contributions are more likely to be as adjuncts and suppliers to protected areas and in furthering public education than in protecting nature per se. In part, this is because these institutions are severely limited in the number of species they can house or grow. Frozen collections of gametes, other cells, DNA, etc., have much value for comparative research, but they don't preserve ecological and evolutionary processes.

Unfortunately, the public and the decision makers they elect poorly understand how all of these components are related in an overall conservation strategy. Therefore, conservationists, and their partners (conservation biologists, funders, some philosophers and theologians, etc.), have the additional responsibility of educating decision makers so that their policies are better informed. This a relatively new arena for conservation biologists and one that demands new, bold initiatives.

New Directions in Conservation Biology: Crosscutting Themes

One of the changes that has occurred in conservation biology during the last two decades, and is reflected in the research priorities identified in many chapters of this book, is the growing appreciation of the complexity of interactions in nature and of the varied spatial and temporal scales and contexts in which they operate. Twenty years ago the tendency was to study relatively pristine systems in isolation from the human and global matrix in which

they were imbedded. Today there is a developing awareness of the complex feedbacks at all levels of biological organization, between relatively remote parts of the earth, between developed lands and wildlands, and between human beings and nonhuman biotas.

Complex, multiscale, multidisciplinary, and global interactions have motivated many of the research questions and priorities that are prominent in this volume. For heuristic reasons, here we classify many of the issues under the heading of "crosscutting" themes because they straddle many subdisciplines. Some of these themes, which are now prominent in the thinking of conservation biologists, were hardly mentioned in the earlier volume on this subject (Soulé and Kohm 1989). Therefore, they represent a considerable advance in the field. The most important crosscutting themes include the following:

- positive feedbacks and multiple direct and indirect effects;
- the ecological and cultural context of issues (the "it depends" problem);
- lag effects;
- cumulative effects;
- the role of the "matrix" of inhabited and exploited lands that surround protected areas;
- introduced, invasive exotic species;
- the complexity of pollutants (including such agents as hormonally active substances);
- the role of ecological restoration, particularly at regional scales;
- the identification and use of focal species; and
- monitoring and evaluation.

Although these categories overlap, they nonetheless highlight many of the emerging themes in conservation biology. In the following sections, we elaborate on these themes.

Positive Feedbacks and Multiple Direct and Indirect Effects

The chapters of this book contain frequent references to feedbacks between processes that affect ecosystems and populations at all scales. At the local or population scale, for example, there are interactions between genetics, demography, and environmental variation that affect the viability of populations and that require attention (chapters 2 and 5).

At an intermediate (regional) scale, we are becoming more aware of cascading interactions between trophic levels in food webs and the need to clarify the relative frequencies of strong and weak ecological interactions among species (chapter 3). For example, there is increasing interest in top carnivores and other strongly interacting species and the consequences of their disappearance for the diversity and resilience of ecosystems (Terborgh et al. 1999).

Some conservation biologists are calling for regional and continental networks of wildlands that specifically depend on the stabilizing presence of large carnivores (Soulé and Noss 1998). They are declaring that the current criteria for recovery of endangered species fail to acknowledge the need to restore ecological interactions of "keystone" species throughout much of their former ranges (Soulé, et al. in preparation).

At continental and global scales, conservation biologists are increasingly concerned about the likely interactions between sea surface temperatures in the Pacific (El Niño and La Niña), the devastating fires in tropical rain forests, and the role that logging plays in exacerbating those fires. The possibility that deforestation will cross a threshold that could produce a biologically devastating and economically disastrous decline in precipitation in the Amazon Basin is considered a real one.

Other kinds of complex interactions between spatially separated marine and terrestrial ecosystems are becoming more apparent. The important role of salmon, for example, as conveyors of oceanic nutrients and calories to temperate forests is now gaining attention and causing concern as salmon disappear and nitrogen subsidies from marine to terrestrial ecosystems are reduced. This example is representative of the growing literature on nutrient and organic matter exchanges between ecosystems and on the global transport of pollutants, pathogens, and, possibly, hormonally active substances (chapter 8).

The Ecological and Cultural Context of Issues

Because natural systems (ecosystems) are heterogeneous, infinitely variable, nonlinear, dynamic, open, corruptible by invasion by exotic species, frequently chaotic, and strongly influenced by both nearby and remote processes and human activities, they cannot be managed successfully by a "cookbook" approach. Thus, simple rules of thumb have limited value (chapter 10). This means that conservationists who are designing and managing protected area networks have few useful generalizations available to guide them. And the practice of conservation—not to mention the development of the science that supports it—is likely to become even more complex in the future.

Therefore, the answer to most questions about nature protection is, unfortunately, "It depends." For example, it is evident that the nature and penetration of edge effects depend not only on local human culture but also on landscape characteristics (chapter 5). The "it depends" dilemma plagues ecological management and is one of the reasons for the frequent plea for adaptive management (chapter 10). We hasten to add, however, that this growing realization is healthy, because progress is unlikely if we continue to believe

that complex, embedded systems are amenable to simplistic descriptions and formulaic prescriptions.

For example, conservation biologists are often asked about the ecological and architectural rules that should govern the design and placement of wildlife corridors: how long? how wide? should they follow ridge tops or watercourses? should they provide food and shelter? should they avoid roads and highways? Such obvious questions need to be evaluated and answered in two different ways. One concerns basic biology—that is, the specific functions of the linkages and the natural history of the target species. A useful literature to guide the design of corridors based on biological criteria is rapidly developing (Earn, Levin, and Rohani 2000). Similar issues arise when considering questions related to the design of protected areas.

The other perspective concerns the context—both biophysical and cultural—on which many decisions hinge. For example, even if it were established that individuals of the target species would actually use the corridors, it might not be advisable to establish them because a high potential for poaching, a cultural factor, might exist. If poaching is now (or is likely to become) a threat to the survival of animals using a corridor for dispersal or migration, then human behavior must be considered as a major element in determining the desirability of establishing corridors, their placement, and their dimensionality. Finally, it is necessary to consider how the context, including climate, human technologies, and land uses, might change in the future.

The research priorities identified in some of the previous chapters also reflect the recognition that research results that are fundamentally important for conservation may not be used unless the results are cast in ways that help managers make their on-the-ground decisions. Note in this regard that the Society for Conservation Biology is now publishing a new journal, *Conservation Biology in Practice*, that responds to this need.

Another problem for managers is that the optimal solutions suggested by basic research may not be feasible for a variety of reasons. Therefore, managers need help in using scientific information to make choices from among the set of suboptimal options available to them. In other words, conservation biologists need to frame their theories and empirical results in ways that deliver effective decision-making tools that can be used by managers (chapters 2 and 10). This is a major challenge in conservation biology.

Lag Effects

There is increasing recognition that many of the consequences of land conversion and environmental change do not materialize until well after the changes have happened. That is, there are often important lag effects. For example, small, isolated populations of long-lived species may not actually

disappear for decades after their fate has been sealed (chapters 2, 3, and 5). And exotic species may not become invasive for several years or decades after being introduced (chapter 4). Moreover, the indirect, cascading effects of extinctions may not be detectable for long periods (chapter 3). In the oceans, the disappearance of large pelagic fish and great whales, resulting from overfishing, including bycatch, can cause systems to switch between stable states, effects that may also have long lags (e.g., chapter 7). Decision-theory approaches can provide guidance where the consequences of management actions and inactions are expressed only after long delays. For example, a fire suppression policy has serious consequences, but they may not be expressed in time for human intuition to perceive, much less provide, useful solutions to them (chapter 10).

Cumulative Effects

Most environmental problems are not generated primarily by single large perturbations—the smoking gun scenario. Rather, they are the result of many, often unrelated, insults that combine to cause major changes—the “death from a thousand small wounds” syndrome. Acid precipitation is caused not by the discharges from one power plant but by the discharges from many of them. Extinction is caused not by the alteration of one small tract of land but by the progressive loss of habitat, small piece by small piece. Government agencies that manage public lands often ignore deleterious and additive or multiplicative impacts caused by different kinds of land-use practices, or spillover effects on adjacent lands. Instead, agencies tend to focus on the potential short-term effects of a new proposal or use of a particular site (chapter 2). Different kinds of disturbances may also combine to yield deleterious effects that are more serious and qualitatively different from the effects caused by any one of them. In the seas, cumulative effects are often the consequence of overfishing combined with pollution, and exacerbated by pathogens that may be more virulent in physiologically weakened hosts (chapters 7 and 8).

The Role of the “Matrix” of Inhabited and Exploited Lands That Surround Protected Areas

One of the consequences of the rapid growth in human numbers is a general ecological deterioration of the so-called matrix lands that support the human economy and that surround protected areas. These areas have the potential to support many species and are, therefore, relevant components of effective conservation strategies. Unfortunately, matrix lands are being converted into ecological sinks for most species (chapter 5). In the oceans, overfishing by both

industrially advanced and impoverished developing nations is devastating huge areas on continental shelves, and coral reefs are being destroyed by the use of dynamite, cyanide, and bleach fishing (chapter 7).

Nonprotected areas may be managed so intensively for production of marketable commodities that little habitat remains for wildlife, and what habitat exists is increasingly harsh. Moreover, the new communication technologies that allow people to carry on their professional activities from rural areas such as Bozeman, Montana, for example, and the wealth that enables people to build vacation homes in such remote places are contributing to a new kind of sprawl (e.g., “ranchette pox” or “bungalow blight”) that is more detrimental to wildlife than the farms and ranches it is replacing. These forces, in addition to ordinary uses of matrix lands, including agricultural intensification, are reducing the utility of buffers around protected areas.

Introduced, Invasive Exotic Species

Many observers believe that invasive exotic species are overtaking habitat loss and fragmentation as the major threat to biodiversity. Combating invasive species is one of the most challenging problems faced by marine, aquatic, and terrestrial conservationists (chapters 4, 6, and 7). We still understand too little about the dynamics and interactions of invaders and how they come to dominate ecosystems. And there is increasing concern about species used in mariculture, whether or not they have been genetically modified, that are cultivated in areas remote from their native ranges. For example, Atlantic salmon, which are farmed extensively on the Pacific Coast of North America, have escaped in large numbers, and reproductively mature individuals are now found in some of the region's rivers.

The Complexity of Pollutants

As noted above, pollutants can sometimes exacerbate other drivers (climate change, disease) in the destruction of biodiversity. We need to know more about how pollutants affect food webs (chapter 3) and ecosystem productivity. The oceans are the ultimate recipients of materials introduced into terrestrial and freshwater ecosystems. Coastal and continental-shelf marine ecosystems receive large quantities of materials derived from agricultural lands, among which nitrogen is especially important. In some places the resulting eutrophication is producing expanding dead zones of decomposing algae and plant material (chapters 6, 7, and 9). The threats to birds and other organisms from persistent pollutants are increasing in many parts of the world. And we know far too little about the ecological consequences of industrial chemicals, including the constituents of plastics (chapter 8).

The Role of Ecological Restoration, Particularly at Regional Scales

Restoration ecology is an increasingly important discipline, and attention is shifting from restoring relatively small, highly disturbed sites, where non-native plants were frequently used, to restoring natural assemblages and interactions of species over large areas (chapter 11). Increasingly, the focus in conservation will be restoration at regional scales (Ricketts et al. 1999; Simberloff et al. 1999), the reintroduction of native animals having large spatial requirements, the effects of large-scale disturbances on food webs (chapter 3), and jurisdictional issues between agencies with overlapping responsibilities (chapter 10).

The Identification and Use of Focal Species

There is increasing interest in how to identify and use organisms that can serve as surrogates for the integrity, diversity, and resilience of ecosystems (chapter 2). Although current methods are varied and in a state of flux, species judged to be useful include those that signal habitat quality, keystone species (chapter 3), umbrella species, flagship species (chapter 2), and sentinel species (for early detection of new diseases, chapter 8). Focal species are also increasingly used as key elements in monitoring protocols (chapter 10).

Monitoring and Evaluation

Long-term monitoring is known to be essential for detecting trends, identifying emerging problems, testing hypotheses, and evaluating the efficacy of management interventions, but proposals for funding long-term monitoring are often not competitive with requests for experiments designed to advance the frontiers of knowledge. Fortunately, long-term monitoring is likely to receive increasing support because of the capabilities of new remote sensing and spectral analysis technologies. Some of these technologies are likely to be quickly adopted for monitoring ecological changes (chapter 10). For a few remotely sensed measurements, twenty-five-year time series of high-quality data of nearly global coverage already exist (NRC 2000a). For measurements over large spatial scales, remote sensing offers, for the first time, an affordable means of sampling.

Research Priorities as Checklists for Conservationists

We stated above that the complexity of nature severely limits the types and scopes of useful generalizations that are likely to be generated by conservation biology research in the near future. So, while the unsatisfying answer "It depends" will persist, it behooves conservation biologists to point out, as well, that the relevant variables and conditions (that "it depends" on) are accessible; they are often obvious to competent ecologists and wildlife biologists. In fact,

the research priorities found at the end of each of the core chapters in this book can be easily converted to checklists of factors that should be considered by designers and managers of protected areas when faced with conservation problems. Therefore, conservationists can use this book as a guide to the factors and phenomena that are likely to be germane to their work, even if the chapters do not offer simple answers to the questions being asked.

The Sociopolitical Context in Which Research Priorities Are Implemented

Scientists, such as the authors of this book, who think about research priorities for conservation biology, assume that good science is necessary, or at least helpful, for good conservation. And many scientists believe that they are the ones to decide on the ranking of research questions. Certainly, a consensus on research priorities can advance the field by guiding the funding decisions of private and public foundations looking for ways to leverage dollars into knowledge that will help save nature during the current human-caused sixth huge extinction event. In addition, research priorities aid both young, passionate conservation biologists and older ecologists who are in a state of despair because their discipline is rapidly losing its subject matter.

Nevertheless, it is neither the scientists nor the on-the-ground conservationists who decide what research will be funded. Actually, the relative priorities of research themes identified by scientists typically are only one, and a minor one at that, of the inputs to the processes by which research funds are allocated. In democratic societies, politicians are charged with making such decisions.

Most readers of this book believe that knowledge—and, therefore, research—is a good thing. It is well to bear in mind, however, that this attitude is not universal. People's decisions can be more strongly motivated by expediency and self-interest than by knowledge, especially when the facts do not support their beliefs and desires. Politicians are lobbied every day to ignore the best science available because the answers given by science do not always serve vested interests. Because politicians respond to pressures from multiple agendas that have different levels of financial backing, the discourse on national research priorities is often dominated by fear and short-term (getting reelected and the desire for control) and longer-term exigencies (security, and healthy, long lives). These pressures result in much more research money being allocated to studies on human diseases and weaponry than to solving environmental problems. This is one of the reasons most scientific disciplines have found it necessary to have offices in national capitals.

Most scientists, either by choice or by default, are poorly informed about political processes. They may grumble about the shortage of research funds;

they may even be indignant that funding agencies and foundations don't share their views. Sadly, though, few scientists engage in political processes directly. There are many reasons for this reluctance, some of them good ones. But the cost of scientists' withdrawal from politics, whether conscientious or selfish, ignorant or thoughtful, is that policies continue to be more strongly influenced by those who show up when and where decisions are being made. If conservation biologists hope to see their knowledge recognized and their agendas funded, they will have to join other scientists who have learned the truth of the Woody Allen adage that appears at the opening of this chapter.

It is simply not enough for scholars to deliberate and agree on research priorities. They must also organize themselves to lobby for their funding and to educate decision makers about the merits of making scientifically informed conservation and natural resource decisions and also about the costs of failing to do so. A consensus on research priorities is just one step, albeit an essential one, in a more complex sociopolitical process—one that is characterized by multiple agendas and multiple motivations, not all of which are honorable. These elements cannot be eliminated, but they can sometimes be neutralized by an energetic, persistent educational and lobbying campaign.

The point is that unless decision makers are educated (and lobbied) about the long-term benefits of nature-friendly policy options, and thereby develop an appreciation of the ethical, spiritual, psychological, physical, and economic values of nature, they will continue to support programs that are harmful for both society and nature.

Sustainable Development and Conservation

The dominant view in western societies today is that economic growth, provided that it is "sustainable," is essential for raising the quality of life for people. Furthermore, it is widely assumed that encouraging trade is the most powerful way of stimulating economic growth. For the last two decades, the notion of sustainable development has replaced, in international conservation and development circles, the older idea of protected areas—such as national parks—as the mainstay of biodiversity protection. One result is that governments and banks that control development in the tropics and elsewhere are now encouraging the "sustainable use" of protected areas, and the extraction of commodities from them for the global market, notwithstanding the rapid accumulation of evidence that exploitation and protection may, in many cases, be incompatible (Terborgh 1999).

For example, currently, there is a movement in the New World tropics to subsidize the colonization of national parks by rural and indigenous peoples. This exacerbates the problem that many national parks are "paper parks" that lack effective enforcement of laws and regulations essential for their pro-

tection. At the same time, tropical forests within a few kilometers of roads are silenced by the extirpation of primates, birds, and other edible, marketable animals (Redford 1992).

Thus, although free trade and economic growth have the potential to serve conservation agendas, they have equally great potential to undermine efforts to preserve Earth's biodiversity. Currently, the latter process is dominant. A frequent consequence of free trade is the conversion of important ecosystems (such as coastal estuaries and tropical forests) to aquaculture or livestock growing. The destruction and degradation of these habitats often are irreversible. In addition, economically driven decisions are tacitly made to maximize short-term profits, whether or not they are accompanied by unsustainable practices.

Sustainability is an essential vision for the future relations between humankind and its environment. It is yet to be shown, however, that sustainable development, as currently financed and practiced by institutions engaged in international lending and development assistance, is benefiting nature. Most surveys suggest the opposite (see Soulé 2001 for a review). It is time for conservation biologists to speak out on this subject, arguing constructively for the kinds of institutions and facilities that will be needed to minimize the grievous destruction being caused by population growth, rapidly proliferating technologies, and an increasingly globalized economy.

The Future

Even though human behavior poses the fundamental threat to biodiversity preservation, only people can act to reduce the threats to Earth's biodiversity. Therefore, we believe that there is a need for another workshop and book of this kind that focuses explicitly on the "human dimension" of the biodiversity-nature crisis. This will be a difficult workshop because the social and economic challenges (poverty, disease, injustice, corruption, collapsing infrastructure, fatalism, and so on) are formidable. Moreover, there is a tendency for discussions of the human dimension of biodiversity to be politicized by creeping anthropocentrism—to shift from discussions of what is best for nature to what is best for indigenous and poor people. In a world where human beings receive more than 99 percent of the development aid and charity, it is increasingly difficult to find resources to help the other species with whom we share the earth.

Fortunately, there are many opportunities that could be explored during such a workshop on research priorities in the human dimensions of conservation. For example, some parts of the world are becoming depopulated as global economic pressures, soil degradation, and water supply problems stimulate human emigration from those areas. Eastern and central Europe

and parts of the U.S. plains and short-grass prairies, for example, will offer many options for conservation as people vacate rural areas. Moreover, some governments are creating positive incentives for land-owning communities and individuals to become better stewards of their land.

Opportunities also exist to build upon some promising initiatives that are beginning to explore more creative ways in which to harness market forces to assist conservation (Daily 1997; Daily et al. 2000). In May 2000, an Australian firm called Earth Sanctuaries, Ltd., was listed on the Australian Stock Exchange (see www.esl.com.au), becoming the world's first conservation company to go public. The company buys up land (90,000 hectares as of July 2000) and restores native vegetation and wildlife. It earns its income from tourism, consulting, and sales of wildlife products. The company lobbied for and won a change in Australian accounting law so as to include its rare native animals as assets. The Sydney Futures Exchange is positioning itself to be a global leader in the trading of ecosystem services, including carbon sequestration and nontraditional environmental products such as credits for clean water and biodiversity.

In Costa Rica, which has long been a leader in devising imaginative conservation policies, the government has been paying landowners for such ecosystem services as carbon sequestration, watershed protection, preservation of biodiversity, and scenic beauty. The payments are financed in part by a tax on fossil fuels and are achieving significant conservation and restoration of forests (Castro et al. 1998). Costa Rica has also sold carbon sequestration credits to several European countries (Gámez 1999).

Assigning value to nature's various services provides a way of organizing information (Baskin 1997), but it is only one of many tools that need to be employed in making decisions in today's complex political climate. However, even approximate estimates of value may suffice to identify those initiatives for which the benefits greatly outweigh the costs, such as preserving a natural watershed rather than building a water filtration plant (Chichilnisky and Heal 1998; NRC 2000b), and, hence, to provide powerful advice to municipalities. In addition, such initiatives are stimulating development of integrated ecological-social-economic approaches to managing environmental assets. The future potential of these approaches is substantial.

These and other promising governmental and nongovernmental initiatives are growing rapidly and are receiving increasing support from the private sector. There is no reason to believe that the initiatives that have been tried so far exhaust the possibilities. There are, to be sure, risks associated with putting price tags on nature, and extreme care must be taken to ensure that these initiatives really serve the purpose for which they are intended (Daily 1997). However, the alternative is to continue with what has been the

implicit value heretofore placed on nature's services, namely that they have no value, that they are "free."

Encouraging signs also are provided by current trends in several areas of environmental research. Physical and biological scientists are joining together to craft the new discipline of earth system science (Jacobson et al. 2000), a field that employs powerful analytical techniques to analyze environmental processes at large spatial and temporal scales. Ecologists are also directing more attention to the study of patterns and processes at large spatial scales, a field known as macroecology (Brown 1995; Maurer 1999). These efforts are developing solutions to a major problem, namely that of the high standards for experimental design and adequate controls that legitimately dominate thinking in small-scale science being incompatible with the kinds of research necessary to understand large-scale patterns.

For example, there is no controlled way to manipulate the biodiversity of a large region even if it were morally defensible to do so. Much of the most important work done in conservation biology is based on large-scale studies for which controls are virtually impossible. Studies of top-down regulation by keystone species have to be carried out over many years and over large areas. Studies of the factors affecting the decline in salmon include variables such as fishing pressure for which there can be no replication. Studies of ecological restoration at a regional scale cannot be controlled adequately.

These problems are not unique to earth system science, ecology, or conservation biology. They apply equally, for example, to astronomy, but this has not prevented astronomers from learning a great deal about stars, solar systems, and galaxies. Astronomy owes its success to its strong theoretical foundation in physics, on the basis of which testable predictions are made about the patterns to be expected in complex galaxies. Similarly, ecology and conservation biology, fields that have a strong theoretical foundation in behavioral and population ecology, are now poised to make testable predictions about macroscopic patterns in nature. We earnestly hope that the concepts and ideas in this book will help us make rapid progress in that direction.

LITERATURE CITED

- Baskin, Y. 1997. *The Work of Nature*. Washington, D.C.: Island Press.
- Brown, J. H. 1995. *Macroecology*. Chicago: University of Chicago Press.
- Castro, R., F. Tattenbach, L. Gamez, and N. Olson. 1998. The Costa Rican Experience with Market Instruments to Mitigate Climate Change and Conserve Biodiversity. Fundecor and MINAE, San Jose, Costa Rica.
- Chichilnisky, G., and G. Heal. 1998. Economic returns from the biosphere. *Nature* 391:629–630.

- Daily, G. C. (ed.). 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Washington, D.C.: Island Press.
- Daily, G. C., T. Söderqvist, S. Anlyar, K. Arrow, P. Dasgupta, P. R. Ehrlich, C. Folke, A. Jansson, B.-O. Jansson, N. Kautsky, S. Levin, J. Lubchenco, K.-G. Mäler, D. Simpson, D. Starrett, D. Tilman, and Brian Walker. 2000. The value of nature and the nature of value. *Science* 289:395–396.
- Earn, D. J. D., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. *Science* 290:1360–1364.
- Gómez, R. 1999. *De Biodiversidad, Gentes y Utopías*. Santo Domingo, Costa Rica: INBio.
- Groom, M. J., D. B. Jensen, R. L. Knight, S. Gatewood, Lisa Mills, D. Boyd-Heger, L. S. Mills, and M. E. Soulé. 1999. Buffer zones: Recognizing the benefits and dangers of compatible stewardship. In M. E. Soulé and J. Terborgh (eds.), *Continental Conservation: Scientific Foundations for Regional Conservation Networks*, pp. 171–198. Washington, D.C.: Island Press.
- Jacobson, M. C., R. J. Charlson, H. Rodhe, and G. H. Orians (eds.). 2000. *Earth System Science: From Biogeochemical Cycles to Global Change*. New York: Academic Press.
- Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243–253.
- Maurer, B. A. 1999. *Untangling Ecological Complexity: The Macroscopic Perspective*. Chicago: University of Chicago Press.
- NRC (National Research Council). 2000a. *Ecological Indicators for the Nation*. Washington, D.C.: National Academy Press.
- NRC (National Research Council). 2000b. *Watershed Management for Potable Water Supply*. Washington, D.C.: National Academy Press.
- Redford, K. H. 1992. The empty forest. *BioScience* 42:414–422.
- Ricketts, T. H., E. Dinerstein, D. M. Olson, and C. J. Loucks. 1999. *Terrestrial Ecoregions of North America: A Conservation Assessment*. Washington, D.C.: Island Press.
- Scott, J. M., R. J. F. Abbitt, and C. R. Groves. 2000. What are we protecting? *Conservation Biology in Practice* 2(1):18–19.
- Simberloff, D., D. Doak, M. Groom, S. Trombulak, A. Dobson, S. Gatewood, M. E. Soulé, M. Gilpin, C. Martinez Del Rio, and L. Mills. 1999. Regional and continental restoration. In M. E. Soulé and J. Terborgh (eds.), *Continental Conservation: Scientific Foundations for Regional Conservation Networks*, pp. 65–98. Washington, D.C.: Island Press.
- Soulé, M. E. 2001. Does sustainable development help nature? *Wild Earth* (Winter): 56–64.
- Soulé, M. E., J. Estes, J. Berger, and C. Martinez del Rio. In preparation. Ecologically effective population size and distribution.
- Soulé, M. E., and K. A. Kohm. 1989. *Research Priorities for Conservation Biology*. Washington, D.C.: Island Press.
- Soulé, M. E., and R. K. Noss. 1998. Rewilding and biodiversity as complementary tools for continental conservation. *Wild Earth* (Fall):18–28.

- Soulé, M. E., and J. Terborgh. (eds.). 1999. *Continental Conservation: Scientific Foundations of Regional Reserve Networks*. Washington, D.C.: Island Press.
- Terborgh, J. 1999. *Requiem for Nature*. Washington, D.C.: Island Press.
- Terborgh, J., J. A. Estes, P. C. Paquet, K. Ralls, D. Boyd-Heger, B. Miller, and R. K. Noss. 1999. Role of top carnivores in regulating terrestrial ecosystems. In M. E. Soulé and J. Terborgh, (eds.), *Continental Conservation: Scientific Foundations of Regional Reserve Networks*, pp. 39–64. Washington, D.C.: Island Press.

ABOUT THE CONTRIBUTORS

Michael E. Soulé is professor emeritus in environmental studies, University of California, Santa Cruz, and science director of the Wildlands Project. His Ph.D. in biology is from Stanford University and his research interests include island biogeography, community ecology, and conservation genetics. He was founder of the Society for Conservation Biology and the Wildlands Project. He has written and edited nine books on biology, conservation biology, and the social context of conservation. He is a fellow of the American Association for the Advancement of Science, has received a Guggenheim Fellowship, is the sixth recipient of the Archie Carr Medal, and was named by *Audubon* magazine in 1998 as one of the one hundred Champions of Conservation of the 20th century.

Gordon H. Orians, an ecologist, is professor emeritus of zoology at the University of Washington in Seattle. He received his B.S. in zoology from the University of Wisconsin, Madison, and his Ph.D. in zoology from the University of California, Berkeley, in 1960. His research has focused on the behavioral ecology of vertebrates (foraging, habitat selection, mate selection, and relationships between social systems and the environment), the structure of ecological communities, and the science-policy interface. He was director for eleven years of the Institute for Environmental Studies at the University of Washington, and serves on the board of directors of the World Wildlife Fund–U.S. He is an elected member of the National Academy of Sciences and the American Academy of Arts and Sciences.

A. Alonso Aguirre, D.V.M., M.S., Ph.D., is director for conservation medicine at Wildlife Trust and affiliated professor at Tufts and Columbia universities. Dr. Aguirre is former health director for Protected Species Investigation for the National Marine Fisheries Service in Hawaii. His professional interests include wildlife epidemiology, conservation medicine, and international training of conservation biologists and wildlife veterinarians.

Sandy Andelman is deputy director of the National Center for Ecological Analysis and Synthesis and adjunct associate professor in the Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara. She served as secretary of the Society for Conservation Biology and currently is a member of the editorial board for *Conservation Biology*.

Jonathan Baillie is a Ph.D. student based at the Institute of Zoology, Zoological Society of London, and at Imperial College, London. His research focuses on the extinction filter role humans have played in the process of colonizing oceanic islands, as well as the ecological and evolutionary traits that make some species more vulnerable than others to human threats.

Steven R. Beissinger is an associate professor of conservation biology in the Department of Environmental Science, Policy, and Management at the University of California, Berkeley, where he teaches courses in conservation and population biology. Beissinger studies the behavior, demography, and population viability of threatened and exploited birds. He instructs training courses in small-population biology for the U.S. Fish and Wildlife Service.

P. Dee Boersma is professor of zoology at the University of Washington and the past president of the Society for Conservation Biology. She studies Magellanic penguins at Punta Tombo, Argentina, and other seabirds to understand environmental variation and perturbations. She is a fellow of the American Ornithology Union and AAAS, a member of the advisory board of the Puget Sound Environmental Learning Center, and a member of the Peregrine Fund Board.

James S. Clark is professor of biology in the Division of Earth and Ocean Sciences at Duke University, where his research focuses on how global change affects forests and grasslands. Clark received a B.S. in entomology from the North Carolina State University (1979), an M.S. in forestry and wildlife from the University of Massachusetts (1984), and a Ph.D. in ecology from the University of Minnesota (1988).

Alan Covich is professor of fishery and wildlife biology at Colorado State University. He is past president of the American Institute of Biological Sciences and the North American Benthological Society and is an AAAS fellow. He studies food-web dynamics of temperate and tropical streams and has investigated the benthic-community response to drought and hurricane disturbances in Puerto Rico for the last twelve years as part of the Long-Term Ecological Research Program.

Carla M. D'Antonio is an associate professor in the Department of Integrative Biology at UC Berkeley. She completed her dissertation research at UC Santa Barbara and has worked on the dynamics and impacts of plant invaders in California and Hawaii for fifteen years as both an academician and a professional biologist. She has served on several advisory boards related to the research and management of invasive species.

Kendi F. Davis is a postdoctoral fellow in sustainable ecosystems at the Centre for Arid Zone Research in Alice Springs, Australia. She spends the southern summer studying the ecology of Antarctic islands. She has a B.Sc. (1993) and a Ph.D. (1999)

from the Australian National University. Her current research interests are the management of fragmented landscapes, beetle ecology, and the ecological dynamics of Antarctic islands.

Julie S. Denslow is research ecologist and leader of the Invasive Species Unit with the Institute of Pacific Islands Forestry, USDA Forest Service, Hawaii. She is past president of the Organization for Tropical Studies and the Association of Tropical Biology. She has worked for many years on the dynamics of neotropical forests in Costa Rica and Panama and more recently on invasive plants in tropical and warm temperate forests.

Andy Dobson teaches conservation biology and the ecology of infectious diseases at Princeton University and undertakes research in Scotland, East Africa, and Yellowstone in conservation biology and the ecology of infectious diseases. His current research focuses on the role of pathogens in natural ecological systems and on how the geographical distribution of biodiversity determines both threats and conservation solutions.

Claude Gascon is the vice president for Field Support Programs at Conservation International. Previously, he was the project director and Scientific Coordinator for the Biological Dynamics of Forest Fragments Project in Brazil. He studies Amazonian biodiversity, especially amphibians. His publications encompass conservation and forest management in the Amazon and wildlife management.

Mark A. Hixon is professor of marine ecology and conservation in the Department of Zoology at Oregon State University. His research focuses on the processes driving and regulating population dynamics of reef fishes, as well as the natural mechanisms that maintain biodiversity on reefs. His current conservation interest is marine reserves, especially on coral reefs and along the West Coast of the United States.

Karen Holl is an assistant professor in the Environmental Studies Department at the University of California, Santa Cruz. She studies ecosystem recovery from both natural and human-caused disturbances and uses what she learns to restore ecosystems. She has done research in a range of ecosystems, including eastern hardwood forest, tropical rain forest, California chaparral, grassland, and riparian systems.

Malcolm "Mac" Hunter is the Libra Professor of conservation biology in the Department of Wildlife Ecology at the University of Maine. He is president of the Society for Conservation Biology, a Pew Conservation Fellow, and the author of five books.

Georgina Mace is the director of science at the Institute of Zoology, Zoological Society of London. She has worked extensively on the development of systems for assessing the degree of threat faced by wild species, especially in relation to the IUCN Red List. She now studies the evolutionary aspects of species extinction, especially the biological traits that make species more vulnerable to extinction pressures.

Jim MacMahon is a professor of biology and vice president for university advancement at Utah State University. He is a past president of the Ecological Society of

America, a fellow of AAAS, and a member of several National Research Council committees as well as the Board on Environmental Studies and Toxicology. He studies plant-animal interactions, disturbances in deserts and subalpine areas, and restoration of anthropogenic disturbances such as strip mines.

Chris Margules is officer in charge of the CSIRO Tropical Forest Research Centre and leader of the Sustainable Ecosystems Tropical Forest Ecology Program at Atherton in Queensland, Australia. He is also deputy CEO of the Rainforest Cooperative Research Centre, based in Cairns, Queensland. His current research interests are systematic conservation planning and reintegrating fragmented landscapes.

Laura A. Meyerson is an adjunct assistant professor in ecology and evolutionary biology and environmental studies at Brown University. She studies the ecosystem-level effects of biological invasions and the role of foundation species in ecological restoration. She is a Switzer Environmental Fellow and the author of a review paper for the Ecological Society of America on research priorities for introduced species in the United States.

Fiorenza Micheli is assistant professor of biological sciences at Hopkins Marine Station, Stanford University. She is a marine community ecologist, with a focus on the ecology and conservation of coastal marine ecosystems. Her research interests include species interactions and food-web dynamics in aquatic ecosystems, the effects of multiple disturbances on populations and communities, the conservation and restoration of marine habitats and species, and the design and evaluation of marine protected areas.

Jaqueline E. Mohan earned her baccalaureate degree at the University of Chicago, and her master's of environmental management (MEM) at Duke University, where she is currently in the pursuit of her doctorate in the Department of Biology. Her research focus is the role of biodiversity in terrestrial ecosystems.

Barry Noon is a professor in the Department of Fishery and Wildlife Biology and the Graduate Degree Program in Ecology at Colorado State University in Fort Collins. He studies conservation planning for threatened and endangered species, science-based management of public lands to conserve biological diversity, population dynamics and viability analyses for at-risk species, vertebrate demography and life history, and methods to study natural populations of vertebrate wildlife, ecological monitoring, and biometrics.

Elliott A. Norse is president of Marine Conservation Biology Institute and is a marine and forest conservation biologist. He defined the concept of biological diversity in 1980 and now focuses on creating a comprehensive national network of fully protected marine reserves to protect marine biodiversity.

Richard S. Ostfeld is associate scientist and animal ecologist at the Institute of Ecosystem Studies in Millbrook, New York. His research focuses on linkages between community ecology and the dynamics of infectious diseases. Current projects include the impacts of reduced species diversity on transmission of Lyme

disease and other vector-borne diseases, and how forest fragmentation influences communities of hosts for ticks.

Gary Allan Polis was professor and chair of the Department of Environmental Sciences and Policy of the University of California, Davis. He made major contributions to the theory and empirical study of food webs, particularly on the roles of spatial subsidies, cannibalism, and intraguild predation in food-web dynamics. He did extensive work on the ecology of island and desert communities in California, Mexico, and Namibia, and he was a world authority on scorpion and spider ecology. Gary died in the spring of 2000 during a tragic boating accident in the Gulf of California.

Mary Poss, D.V.M., Ph.D., is a member of the faculty of the Division of Biological Sciences and the Wildlife Biology Program at the University of Montana. She is a veterinary pathologist and has degrees in biochemistry and experimental pathology. Her areas of research include virus evolution, ecology, and pathogenesis.

Hugh Possingham is professor of zoology and mathematics and director of the Ecology Centre at the University of Queensland, Australia. He is a population modeler and ecological theorist with a particular interest in applications of decision theory to conservation biology. Among a variety of public service and advocacy roles, he is the chair of the national Biological Diversity Advisory Committee in Australia.

H. Ronald Pulliam is Regent's Professor of Ecology at the University of Georgia. His major research contributions have been in the areas of biological diversity, community ecology, behavioral ecology, source-sink theory, and population dynamics in heterogeneous landscapes. He has also served as president of the Ecological Society of America, science advisor to the United States Secretary of Interior, and director of the National Biological Service.

Kent H. Redford is director of biodiversity analysis and synthesis for the Wildlife Conservation Society based in New York. Prior to that he directed the Conservation Science and Stewardship Program of The Nature Conservancy's Latin American and Caribbean Division and taught at the University of Florida. His interests are in park-based conservation, subsistence use of wildlife, and resource use by indigenous peoples.

Chantal D. Reid is a research scientist in the Department of Biology at Duke University, where she is studying direct effects of elevated CO₂ and tropospheric ozone on plant growth and productivity. She received a B.Sc. in biology from McGill University (1980), an M.S. in biology from San Diego State University (1985), and a Ph.D. in botany from Duke University (1990).

William H. Schlesinger is James B. Duke Professor of Biology at Duke University, where he holds a joint appointment in the Division of Earth and Ocean Sciences and the Nicholas School of the Environment. He studies global biogeochemical cycles, focusing on the response of soils in global change. He received an A.B. from Dartmouth College in 1972 and a Ph.D. from Cornell University in 1976.

Paul Snelgrove is an associate chair in Fisheries Conservation at Memorial University of Newfoundland in Canada. He studies the early life histories of marine organisms, particularly the invertebrates that live in sediments and the factors that regulate their diversity.

Gary Tabor, a wildlife veterinarian and an ecologist, is head of the Wilburforce Foundation's Yellowstone to Yukon Program, which promotes science and conservation to maintain ecological connectivity in the Rocky Mountain region of the United States and Canada. He served as founding director of the Center for Conservation Medicine, an ecological health collaborative. His international conservation background includes seven years in East Africa and a year each in Latin America and Asia.

Steve Trombulak is a professor of biology and environmental studies at Middlebury College in Vermont. His research includes topics in ecological reserve design, vertebrate ecology, and conservation education. He is also interested in the role of conservation biology in conservation advocacy.

Diana Wall is professor and director of the Natural Resource Ecology Laboratory, an international ecosystem research center at Colorado State University, and past-president of the Ecological Society of America, the American Institute of Biological Sciences, and the Society of Nematologists. She studies the consequences of human activities on soil sustainability in agricultural, grassland, and Antarctic ecosystems.

INDEX

- Abundance: ecological health and, 158; of exotic species, 43, 66; in food webs, 33; fragmentation of habitat and, 85, 86, 88; global environmental change and, 175, 179, 184, 186, 192, 193, 202; in marine ecosystems, 138; in soil and sediment habitats, 100; species at risk and, 15, 34, 37, 42–43
- Abutilon theophrasti*, 188
- Abyssal plain, 129
- Acid rain, 194–197, 276
- Adaptation, 16, 18, 19, 66, 253–254
- Adaptive management, *box* 22, 23–24, 45, 274; in marine ecosystems, 140–142, 144
- Aedes japonicus*, 160
- Africa, 18, 159, 197
- Agriculture: Australian wheatbelts, 81, 87–89, 92; exotic species and, 61–62, 65; pollutants, 37, 43, 110–111, 132, 197; soil invertebrates and, 100–102
- Air quality standards, 196
- Alaska, 41, 136, 184, *figure* 185
- Algae, 41, 202
- Algal blooms, 39, 111
- Allee effect, 62, 136
- Allopatric species, 181
- Alps, 81, 180, 181, 184
- Amazon rain forests, 81, 86, 87, 88, 110, 274
- Ambient treatment, 190, 202
- Ammonia, 195
- Amphibians, 11, 195, 202, 246
- Antarctica, 40, 195, 201
- Aphids, 199
- Appalachians, 181
- Aquaculture, 101, 109, 168
- Aquariums, 109, 137
- Aquatic ecosystems. *See* Marine ecosystems
- Arabidopsis thaliana*, 69
- Aragonite, 193
- Architecture, community, 252–253, 275
- Arctic, 175, 184
- Argentina, 88, 202
- Argentine ant, 83
- Arid regions, 112, 179, 182, 183
- Arizona, 186
- Arthropods, 159, 161, 195
- Ash populations, 199
- Asia, 18
- Asian clam (*Potamocorbula amurensis*), 110
- Asian mitten crab (*Eriocheir sinensis*), 62
- Aspen, 198
- Assembly rules, 250–251

- Assessment: in conservation medicine, 164–165, 169; for exotic species, 71, *box* 73; for food-web alteration, 41–46; global environmental change and, 202–203; for marine ecosystems, 130–131, 133–134, 138; for species at risk, 11–19
- Atherton tableland, 182
- Atlantic salmon (*Salmo salar*), 65, 277
- Australasian planarian flatworm (*Artioposthia triangulata*), 109–110
- Australia, 15, 23, 81, 282; southeastern, 83, 88; western, 87–88, 89, 92
- Avian malaria, 66, 157
- Bacteria, 131, 159
- Ballast water, 60, 108–109, 136, 139
- Balsam fir, 39
- Baltic Sea, 137, 182
- Barnacles, 41
- Barndoor skate (*Raja laevis*), 14
- Barriers, 109, 180–182
- Baselines, 6–7, 134–135, 161, 164
- Bears, 40
- Beech: *Fagus grandifolia*, 181; *Fagus sylvatica*, 181, 200
- Beetle species, 83, 86, 89, 180, 199, 251
- Benguela ecosystem food web, 35, *figure* 38
- Benthic communities, 39, 40, 44, 100, 101, 108, 111, 131
- Berberis thunbergii*, 109
- Biodiversity, 3–4, 8, 18; ecological health and, 155, 157–158, 164, 168–169; exotic species and, 60, 63, 74; fragmentation of habitat and, 89, 92; global environmental change and, 6, 175–203, *figure* 177, *figure* 187, *table* 188; in marine ecosystems, 125, *tables* 127, 129, 130–144; in reserves, 271–272; restoration ecology and, 246; in soil and sediment habitats, 99–101, 102, 106–116
- Biogenic habitat builders, 133, 137
- Biogeochemistry, 109
- Biogeography, marine, 132, 133
- Biological control agents, 34, 62, 71
- Bio-manipulation, 33, 35, 43, 44
- Biomarkers, 163–164
- Biomass: global environmental change and, 198, 200; in marine ecosystems, 39, 42–43, 131, 202; in soil and sediment habitats, 110, 192; in trophic cascades, 34, 37, 49
- Biomedical research, 157, 169
- Biota: global environmental change and, 176, 180, 194–197, 201–202; of soil and sediment, 99, 100–101, *table* 106, 109, 111–113
- Bioturbation, 100, 102
- Birch trees, 181, 198
- Birds: ecological health and, 157, 159–160; as exotic species, 62; fragmentation of habitat and, 86, 88; global environmental change and, 19, 175, 183, 186; soil invertebrates and, 110; as species at risk, 15. *See also names of species*
- Bison (Bison bison), 162–163
- Bivalves, freshwater, 108, 110, 112–113
- Black cherry (*Prunus serotina*), 198
- Black-footed ferrets (*Mustela nigripes*), 157
- Black grama (*Bouteloua eriopoda*), 186, *figure* 187
- Black Sea, 41, 137
- Bleach fishing, 137, 277
- Boreal forest, 183, 201
- Bottom-dwelling species, 113, 138
- Bottom-up forces, 32, 33, 36–41, *table* 36, 45, 47
- Bovine brucellosis (*Brucella abortus*), 162–163
- Bozeman, Montana, 277
- Bracken fern (*Brachypodium*), 195
- Brazil, 14, 83, 87, 88
- Brown tree snake, 41, 66
- Burden of proof, 144, 238
- Butterflies, 19, 175, 183, 256, 257
- Bycatch, 39, 139
- C3 plants, 188–189, 191, 200
- C4 plants, 188–189, 200
- Calcium, 196
- California, 64, 83, 88, 134, 136, *figure* 199, 251
- Calluna*, 195
- Calosoma*, 181

- Cameroon, 19, 111
- Canada, 192
- Canada mayflower (*Maianthemum canadense*), 185
- Canine distemper, 157, 162
- Cannibalism, 35
- Canopy, 83, 87, 190, 198
- Cape Cod, 184–185
- Cape Floristic, South Africa, 15
- Captive breeding, 23, 228
- Carbohydrates, 192
- Carbon, 39, 111, 192; storage, 99, 102
- Carbon dioxide: global environmental change and, 6, 108, 112, 175–195, *figure* 191; nitrogen and, 197; ozone and, 200–201; restoration ecology and, 253; UV-B radiation and, 201
- Caribbean, 134, 137, 139
- Carnivores, 16, 34, 35, 39–40, 273–274
- Carpathians, 181
- Cascading effects, 33, 88–89, 113
- Caspian Sea, 110
- Catastrophic change, 16, 23, 67, 109, 116, 165
- Caterpillars, 181
- Cattle, 64, 162–163
- Central America, 18
- Chaco forests, 88
- Checklists, 278–279
- Chestnut blight, 7
- Chihuahuan Desert, 186, 187
- Chipmunks, 183
- Climate change, 6, 19, 23, 176, 202; ecological health and, 156, 161, 164, 168; effect on soil and sediment invertebrates, 100, 112–114; exotic species and, 63; restoration ecology and, 253. *See also* Global environmental change
- Clover (*trifolium repens*), 198, 199, 201
- Coastal areas. *See* Marine regions, coastal
- Coastal sage shrub, 198, *figure* 199
- Coastal Wetlands Planning, Protection and Restoration Act, 261
- Cocinellid beetle, 251
- Coffee plantations, 255
- Colonization: in fragmentation of habitat, 84–86; global environmental change and, 193; restoration ecology and, 249–250, 256; in soil and sediment habitats, 108, 110
- Colorado, 184
- Commercial fishing, 5, 14, 32, 35, 39–40; destructive practices, 101, 136, 137–139
- Community structure: alteration of food webs and, 47; exotic species and, 67, 70; global environmental change and, 176, 178, 194, 200; in marine ecosystems, 135–136, 139; restoration ecology and, 249, 251–253, 255; trophic cascades and, 39–44
- Competition displacement of species: in consumer-resource interactions, 44; ecological health and, 156, 159; exotic species and, 15, 59, 63, 66–67; in food webs, 35, 39, 47; fragmentation of habitat and, 92; global environmental change and, 181, 182, 188–190, 194, 202; in marine ecosystems, 136, 138, 139; restoration ecology and, 252; sediment invertebrates and, 109
- Computer image analysis, enhanced, 114
- Concholepas concholepas*, 40–41
- Congeneric species, 65, 190
- Conifers, 183, 197, 198, 254. *See also names of species*
- Connectivity, 246, 256
- Conservation Biology in Practice*, 275
- Conservation medicine, 155–169, *box* 166–167
- Conservation program planning, 232–233, *figure* 233
- Consumer-resource interactions, 31–36, 44–49, 195
- Continental shelves, 126, 277
- Control protocols, 69–71, 229
- Coral honeysuckle (*Lonicera sempervirens*), 190
- Coral reefs, 5, 8, 19, 50, 101, 125–126, 130, 133, 135–138, 142–143, 184, 193, 277
- Cordgrass, 251
- Corridors, 2, 134, 158, 164, 168, 256, 275
- Costa Rica, 282
- Cougars, 40
- Cover crops, 71

- Cowbirds, 88
 Coyotes, 40, 88
 Crabs, 39, 139
 Crayfish, 11
 Creosotebush (*Larrea tridentata*), 183, 186, *figure* 187
 Crop species, 198, 200
 Crosscutting themes, 272–273
 Crustaceans, 106, 126
 Cryptic species, 131, 134, 139
 Ctenophore (*Mnemiopsis leidyi*), 41
Culex pipiens, 160
 Cultured species, 139; salmon, 65, 139
 Cyanide fishing, 137, 277
- Decision theory, 225–241, *figure* 231, 275–276
 Decomposers, 131, 192
 Decomposition, 102, 112, 140
 Deer, 40
 Deforestation, 274
 Degradation of habitat: ecological health and, 157; exotic species and, 59, 71; extinction risk and, 13; fragmentation and, 82, 87, 88; global environmental change and, 193; in marine ecosystems, 137–138, 142; restoration ecology and, 245, 247; soil and sediment invertebrates and, 101, 109
 Delaware Water Gap, *figure* 177
 Demersal fishes, 131
 Dengue fever, 156
Deschampsia, 195
 Designer communities, 247, 254–255
 Detritivores, 102
 Detritus input or loss, 35, 47, 50, 102, 111; in marine ecosystems, 131
 Diagnostic capability, 165, 168–169
 Diapausing stages, 109
 Diatom communities, 201
 Dioxins, 136, 140
 Disease: ecology of, 155–169, *box* 166–167; exotic species and, 64, 66, 67; global environmental change and, 182; marine ecosystems and, 139
 Dispersal dynamics, 275; ecological health and, 161; fragmentation of habitat and, 84–86, 87; global environmental change and, 179, 181, 182, 186; in restoration ecology, 249, 252–254, 256; for species at risk, 2, 5, 15, 18
 Distributions of species, 3; fragmentation of habitat and, 83, 85; global environmental change and, 175–176, 179, 181–183, 186, *figure* 199; in soil and sediment habitats, 113
 Disturbance: exotic species and, 61; fragmentation of habitat and, 82, 88; global environmental change and, 112, 176; in marine ecosystems, 135, 136, 137, 139; restoration ecology and, 246–249, 253–254, 257; soil and sediment invertebrates and, 99, 100–101, 107, 111, 114
 Disturbance regimes, 67, 70–71, 246, 256
 DNA research, 68, 272
 Dogs, 157, 168
 Domestic animals, 161–165, 168–169
 Dominance–diversity curves: global environmental change and, 180–182, 184, *figures* 185, 187; nitrogen and, 195; Parkgrass experimental plots, 176–178, *figure* 177; tropospheric ozone and, 198
 Dredging, 5, 101, 136, 137
 Drought, 62, 82, 156, 185–186
 Duke Forest FACE, 190, *figure* 191
 Dung beetles, 89
 Dynamic changes, 18–19; fragmentation of habitat and, 84, 86–87, *box* 91
 Dynamite fishing, 136, 137, 277
- Earth Sanctuaries, Ltd., 282
 Earthworms, 109–110; *Pontosclex corethrurus*, 110
 East Africa, 12, 41, 66
 Eastern phoebe (*Sayornis phoebe*), 183
 Ecological assembly rules, 250–251
 Ecological footprint, 155
 Ecological health, 155–169
 Ecological recovery, 247
 Ecology, 82, 92, 133, 157, 161–163, 164, *box* 166–167
 Ecosystems: consumer–resource interactions in, 36–41; exotic species in, 66–68, 70; fragmentation of

- habitat and, 89; global environmental change and, 184–185, 187, *table* 188, 202; management of, 2, 274–275. *See also* Forest ecosystems; Freshwater ecosystems; Grassland ecosystems; Marine ecosystems
- Ecotones, 19
- Ecotourism, 126, 168
- Ectomycorrhizal fungi, 64
- Edge effects, 84–86, 227, 274
- Elasmobranchs, 40
- Elephants, 14
- Elk, 162–163
- El Niño, 274
- Elymus glaucus*, 66, 254
- Endangered species, 6, 23, 59, 274;
 - consumer-resource interactions and, 32; decision theory and, 234;
 - ecological health and, 157, 158–159;
 - in marine ecosystems, 136;
 - restoration ecology and, 246, 256; soil and sediment invertebrates, 108
- Endangered Species Act (U.S.), 2, 59
- Endemic species, 108, 158, 159, 161–162, 165
- Endemism, 15, 17–18, 81, 87; in marine ecosystems, 130, 134
- Enemy-victim models, 33–34
- Epidemic outbreaks, 159
- Epidemiology, 157, 158
- Equilibrium theory, 84
- Erosion, 71, 101, 111; coastal, 136–137, 156
- Establishment, 249
- Estuaries, 111, 126, 136, 142–143, 197, 257
- Eucalypt forests, 83
- Eucalyptus plantations, 87
- Eucalyptus salmonophloia*, 92
- Europe, 18, 68, 81, 109, 159, 180, 181, 182, 198, 282
- Eutrophication, anthropogenic, 8, 33, 35, 39, 43, 44, 111, 139–140
- Evolutionary diversity, 11–12, 18, 19, 179–180, 194
- Exotic species, 5, 6–7, 8, 44, 46, 59–74, 276, 277; consumer-resource interactions and, 33; ecological health and, 158, 161, 162; fragmentation of
 - habitat and, 83, 86, 87; global environmental change and, 182, 190, 197; in marine ecosystems, 132, 136, 139; predators as, 41; restoration ecology and, 250, 254, 262; sediment invertebrates and, 108–109; in trophic cascades, 43
- ex situ* conservation facilities, 272
- Extinction risks, 3–4, 11–24, *table* 12, 276; ecological health and, 158, 159; exotic species and, 5, 59, 65, 66, 67; fragmentation of habitat and, 81–82, 84, 85; global environmental change and, 156, 176, 178, 179, 182, 184, 192, 202; in marine ecosystems, 126, 132, 135–136, 194; restoration ecology and, 246, 250; soil and sediment invertebrates and, 108
- Extirpations, 8, 61, 62
- Fauna, 109, 113, 161
- Feedback loops, 251, 273
- Feeding stations, 158, 163
- Feline immunodeficiency virus (FIV), 163
- Feline leukemia virus (FeLV), 163
- Fender's blue butterfly (*Icaricia icarioides fenderi*), 256, 257
- Fennel (*Foeniculum vulgare*), 64
- Feral cats, 40
- Feral sheep, 64
- Fertilizers: fragmentation of habitat and, 88; global environmental change and, 176, *figure* 177, 195, *figure* 196; in marine ecosystems, 136, 140; soil and sediment invertebrates and, 110–111
- Field experiments: ecological health and, 162; of exotic species, 69; global environmental change and, 176, 184–191, *table* 188, *figure* 191, 194–196, 199–201, 203; in marine ecosystems, 134, 135
- Fire, 82, 87, 89, 274; frequency, 67, 257; management of, 229–232, *figure* 231, 257; suppression, 186
- Fish: extinction risk and, 11–12, 19; in food webs, 39–43; global environmental change and, 195; in marine ecosystems, 130–133, 135;

- Fish (*continued*) overexploitation of, 14, 32; restoration ecology and, 252
- Fisheries, 35, 39, 41, 46, 65, 126, 133, 135, 277; management of, 32, 41, 48, 138–139, 141
- Fishing, 37, 43, 44, 46, 50; commercial. *See* Commercial fishing
- Fish stocks, 132, 135, 136, 139, 141
- Flavonol compounds, 201
- Florida, 64, 257
- Flounder, 40
- Focal populations, 161, 238, 256, 278
- Food and Agriculture Organization (FAO), 14
- Food chains, 34–35, *figure* 37, 46, 100, 110
- Food webs, 8, 31–50, 277; freshwater, 110; global environmental change and, 182; marine, 14, 131, 138; models, *table* 36, 47, 48–49; soil invertebrates and, 111
- Forbs, 191, 198
- Forest clearing, 81, 101, 110, 111
- Forest ecosystems, 189–191, *figure* 191, 196, 197–200
- Forest savannah, 19, 189
- Forest Service (U.S.), 237
- Fossil fuels, 6, 126, 188, 197
- Fossil record, 12–13, 135, 139, 178–180, 182, 255
- Founder effects, 179–180
- Foxes, 40, 41
- Fragmentation of habitat, 3, 4–5, 13, 18, 81–92; decision theory and, 228; ecological health and, 168; global environmental change and, 112, 182; marine, 137–138; restoration ecology and, 256; top carnivores and, 39–40
- Fragment edges, 83–84, 85, 87
- Free-Air CO₂ Enrichment, 190, *figure* 191, 194, 201
- Freshwater ecosystems, 102, *table* 105, 106–107, *figure* 107, 112–113; invasive species in, 110
- Frogs, 86
- Frugivores, 89
- Fuel load, 87, 89
- Fungi, 112, 159, 193
- Fungicides, 111
- Fur seals, South African, 35
- Gadid, piscivorous, 40
- Gastropods, 40–41
- Gatun Lake, Panama, 41
- Gene pools, 65
- Genetically modified organisms (GMOs), 68–69, *box* 74, 139
- Genetic bottlenecks, 62, 161
- Genetic diversity: ecological health and, 159; fragmentation of habitat and, 89; global environmental change and, 179–180, 199; invasive species and, 64–65; in marine ecosystems, 125, 130–131, 134; viral, 163–164
- Genetic effects, 16–17, 64–66, 273; ecological health and, 161; fragmentation of habitat and, 82; restoration ecology and, 253–254
- Genetic research methods, 135–136, 138, 139; ecological health and, 162
- Genetics of Colonizing Species* (Baker and Stebbins), 64
- Genotypes, 66, 68–69, 180, 181, 199, 255
- Geographical distribution of species, 112, 114, 139
- Geographic information systems (GIS), 114, 133–134, 141
- Geological history, 100, 134, 188
- Geomorphology, 258
- Geo-referencing, 114
- Georges Bank, 40, 137
- Georgia, *figure* 196
- Glacial periods, 176, 178–182, 183, 186, 188–189
- Global environmental change, 175–203, *table* 188; ecological health and, 155–156; human activities and, 19, 39, 63, 99; marine ecosystems and, 126, 136–137, 141, 144; soil and sediment invertebrates and, 108–113, 116
- Global positioning systems, 114
- Goals of conservation activities, 6–7, 258–259
- Grasses, 186, 192; fire-enhancing, 67, 87; native, 66
- Grasshoppers, 180–181
- Grassland ecosystems, 4, 184, 191–192,

- 195, 198, 257
 Grazing, 35, 64, 88, 92, 102, 111, 168, 186, 192
 Great auks, 40
 Great Barrier Reef Marine Park, 235
 Great Basin, 186
 Great Britain, 17–18, 62, 109, 176, *figure* 177, 181, 184
 Great Lakes, 7, 109, 110, 182
 Great Plains, 186, 282
 Great tit (*Parus major*), 196
 Greece, 181
 Greenhouse experiments, 189, 190
 Greenhouse gases, 6, 203
 Greenland, 195
 Ground beetle (*Calosoma inquisitor*), 181
 Ground squirrels, 183
 Growing seasons, 184
 Growth rates, 64, 188–195, *figure* 191, 199, 227
 Guam, 41, 66, 71
 Guilds, 250–251
 Gulf of Mexico, 111
 Gypsy moths, 199

 Habitat alteration, 31–50; ecological health and, 157; fragmentation of habitat and, 82–83; marine, 126, 136, 137, 141, 144
 Habitat complexity, 135
 Habitat creation, 247
 Habitat-generating species, 133, 137
 Habitat loss, 4–5, 13–14, 18, 276; ecological health and, 168; extinction risk and, 81; soil invertebrates and, 108, 111–112; top carnivores and, 39, 44
 Halogenated hydrocarbons, 136, 140
 Haplotypes, 180, 181, 182
 Harbaceous species, 185, 199
 Harvard Forest, 185
 Harvesting, 14, 32, 41, 111–112
 Hawaii, 41, 66, 70, 157
 Health sciences, 155–169
 Heath, 81, 87, 195
 Heavy metals, 110, 136, 140
 Helminths, 159
 Hemlock (*Tsuga*), 181
 Herbicides, 69, 111
 Herbivores, 34, 35, 64, 68, 71, 89, 131, 200
 Herbivory, 112, 189, 190, *figure* 191, 199, 249
 Herring, 32, 40
 High-latitude ecosystems, 183–185, 187
 Histopathology, 168
 Holocene, 179, 182, 186, 189
 Hopkins Marine Station (Monterey Bay), 184
 Hormones, endocrine-disrupting, 155, 274
 Horticultural trade, 65
 Host species, 158–159, 160, 161–163, 193
 Human activities, 1, 142; alteration of food webs, 31–50; conservation and, *box* 22, 23; ecological health and, 155–156, 163, 168; exotic species and, 60, 64; extinction risk and, 5–6, 13–19; global environmental change and, 19, 112, 175–176, 178, 182, 194–197, 202; marine ecosystems and, 126, *table* 129, 130, 134, 136–144; restoration ecology and, 253; soil and sediment invertebrates and, 99, 101, 110–111, 113, 116
 Hunting, 14, 37, 39–40, 44, 46
 Hunting dogs (*Lycaon pictus*), 157
 Hybridization, 15, 65–66, 68–69
 Hydrology, 70, 101, 108, 112, 185, 256, 258
 Hydrothermal vents, 130, 134, 193

 Ice age, 178–183, 186, 188–189
 Ice-core evidence, 178, 195
 Immune system response, 156, 159, 161
 Immunodeficiency virus (HIV), 163
 Inbreeding depression, 16
 Indicator species, 237
 Industrial activities, 37, 101, 111, 277
 Industrial Revolution, 188, 197
 Infaunal clams, 137
 Infectious agents. *See* Pathogens
 Infectious diseases, 155–156, 157, 159, 161
 Insect communities, 50, 88, 181, 192
 Insecticides, 68, 159
 Insect resistance, 69

- Interactions among species, 2, 8, 63. *See also* Consumer-resource interactions
- Intergovernmental Panel on Climate Change (IPCC), 175
- International agreements, 14, 202
- Intertidal marine communities, 50, 113, 139, 184
- Introduced species, 3, 5, 23, 276, 277; consumer-resource interactions and, 32; ecological health and, 163, 164; exotic species as, 60–62, *box* 72; extinction risk and, 15; global environmental change and, 182; in marine ecosystems, 126, 136, 139, 144; restoration ecology and, 248, 253–255; soil and sediment invertebrates and, 110. *See also* Exotic species; Invasive species
- Invasive species, 15, 41, 44, 59–74, 276, 277; ecological health and, 161; fragmentation of habitat and, 86, 88; global environmental change and, 190; in marine ecosystems, 139; restoration ecology and, 250, 254, 255, 256, 262; soil and sediment invertebrates and, 108–110, 113
- Invertebrates: freshwater, 11; low-trophic level, 14; marine, 13, 130, 133, 138, 252; mass mortality of, 39; soil and sediment, 99–116, *tables* 103–105, *figure* 107
- Invulnerable life stages, 33, 35
- Irrigation canals, 112
- Island biogeography theory, 84, 226–227
- Island-sea models, 85
- Isle Royale, Michigan, 39
- Isolation of fragments, 82, 84
- Isopoll maps, 180
- Italy, 181
- Japanese honeysuckle (*Lonicera japonica*), 190–191
- Kelps, 39, 125, 138
- Keystone species, 33, 44, 45, 47, 184, 274
- Kissimmee River, 257
- Krill, 40, 135
- Kudzu (*Pueraria labata*), 190
- Lake trout, 183
- Lake Victoria, East Africa, 12, 41, 66
- Landscape-level strategies, *box* 91
- Landscape mosaic, 256–257
- Land-use changes, 15, 18–19, 81, 89, 276; ecological health and, 157, 164, 168; global environmental change and, 202; soil invertebrates and, 111–112
- La Niña, 274
- Larvae, 50, 109, 131, 139
- Larval dispersal, 131–132, 135–136, 141
- Las Cruces, Chile, 40
- Latitudinal gradient, 107
- Leaf conductance, 198–200
- Legislation, conservation, 2, 23, 261
- Lehigh Water Gap, *figure* 177
- Leucaena leucocephala*, 71
- Lichen species, *figure* 177
- Lions, 40
- Loblolly pine (*Pinus taeda*), 190, 201
- Logging, 16, 102, 234, 274
- Long Beach, Calif., 62
- Long-spined urchins, 139
- Los Angeles Harbor, 62
- Lotka-Volterra model, 33–34
- Lyme disease, 156
- Lynx, 164
- Mackerel, 32, 40
- Macroalgal blooms, 140
- Macrofaunal species, 108, 110
- Macroinvertebrates, 102, 184
- Macrophytes, 102
- Malaria, 155, 156
- Malaysia, 81
- Mallee, 81, 87
- Mammals, 86, 179; marine, 126, 131
- Management actions: in consumer-resource interactions, 32–33; decision theory and, 237; ecological health and, 156, 158, 159, 161, 162–164, 168; for exotic species, 69–70; for food-web alteration, 42, 47, 48; for fragmentation of habitat, 89; in marine ecosystems, 132, 140–144; in reserves, 271–272; restoration ecology and, 245–263; for species at risk, 2, 17, 19–24, *box* 21–22
- Management indicator species, 237

- Manaus, Brazil, 83, 88
 Manganese, 126
 Mangoose, 41
 Mangrove habitats, 112, 125–126, 136–138, 142–143
 Mapping in marine ecosystems, 114, 133–134
 Mariculture practices, 136, 137, 139
 Marine conservation biology, 128–144
 Marine ecosystems, 125–144; global environmental change and, 19, 193; restoration ecology and, 246, 247, 249, 252; sediment invertebrates in, 102, *table* 104, 106–109, *figure* 107
 Marine regions, coastal, 126, 134; ecological health and, 168; exotic species in, 50; fisheries in, 135; global environmental change and, 183, 194, 197; habitat alteration in, 136–137; habitat loss and fragmentation in, 4, 83, 88; nutrient enrichment in, 39, 140; sediment invertebrates in, 101, 102, 108–109, 112; trophic cascade in, 39, 42–43
 Marine reserves, *See* Reserves
 Mathematical programming methods, 229
 Matrix lands, 85–89, 92, 256, 272, 276–277
 Meadow grasshopper (*Chorthippus parallelus*), 181
 Medicine, conservation, 126, 155–169, *box* 166–167
 Megafauna, 126
 Melaleuca, 64
 Melanoma, 155
 Mesic valleys, 182
 Mesocosms, marine, 43
 Mesopredator release, 40, 88
 Mesquite (*Prosopis glandulosa*), 186, *figure* 187
 Metapopulation, 85, 131, 135, 164, 262
 Metapopulation theory, 84–85, 226–227
 Mexico, Gulf of, 134
 Microbial blooms, 39, 140
 Microbial communities, 50, 185, 192–193, 200, 202, 251
 Microbial gardening, 102
 Microclimates, 71, 83, 111, 256
Microstegium vimineum, 109
 Middens: human, 139; packrat, 179
 Middle East, 159
 Migration, 35, 175; of birds, 88; corridors, 2, 134, 158, 164, 168, 275; global environmental change and, 180–181, 187; oceanic, 132, 141–142; restoration ecology and, 248–249
 Mineralization, 101, 102, 185
 Mine reclamation, 259
 Miocene, 188, 193
 Mississippi River, 111
 Mixotrophy, 131
Mnemioopsis leidy, 41
 Moisture. *See* Precipitation
 Moisture content of soil, 83, 111
 Molecular analysis, 114, 134, 163, 180, 182
Molinia, 195
 Molluscs, 11
 Monitoring, 278; in conservation medicine, 164–165, 168–169; decision theory and, 225, 235–239; for food-web alteration, 41–46; in marine ecosystems, 133, 134; in restoration ecology, 258–259; for species at risk, *box* 22, 23–24
 Montana, 162, 277
 Montane regions, 182
 Moose, 39
 Mosquitoes, 159–161
 Mosses, 184
 Mountain lions, 164
 Mudsail (*Ilyanassa obsoleta*), 109
 Multispecies communities, 33, 34, 45–46
 Mussels, 41
 Mutations, 16, 64
 Mutualisms, 63, 64, 189, 249
 Mycorrhizal interactions, 193, 249, 253
Myrica faya, 41
 Mysids, 106
Nassella pulchra, 66
 National Center of Ecological Analysis and Synthesis, 248
 National Elk Refuge, Wyoming, 158
 Native species: exotic species and, 5, 8, 15, 41, 59–74; fragmentation of habitat and, 88; global environmental

- change and, 182, 187, 190, 200; in marine ecosystems, 136, 139; restoration ecology and, 251, 254–255; sediment invertebrates as, 109, 110
- The Nature Conservancy, 11
- Nematicides, 111
- Nematodes, 111, 193
- Netherlands, 195, 196
- New England, 40, 109, 137
- New Mexico, 186, *figure* 187
- New York, 109, 159
- New York Times*, 175
- New Zealand, 23, 193
- Nicholson-Bailey model, 34
- Nile perch, 12, 41, 66
- Nitric acid, 195–196
- Nitric oxide, 195, 197
- Nitrogen, 274; availability of, 112, *figure* 177, 178, 185, 194–197, 203, 253; in marine ecosystems, 43, 111, 193
- Nitrogen-fixing ability, 41, 69, 71, 101, 191, 192, 193, 198
- Nitrogenous compounds, 37, 39, 136, 140, 192, 197
- Noninvasive health monitoring techniques, 157
- Nonvascular plants, 184
- North America, 18, 40, 109, 110, 113, 162; central, 186; eastern, 13, 180, 181, 182, 183; northwestern coast, 39; west coast, 277
- Northern cod, 32
- North Sea, 32, 40, 182
- North Sea cod (*Gadus morhua*), 183
- Norway pout, 40
- No tillage, 111
- Null-hypothesis testing, 238
- Nurse-plant effects, 253
- Nutrient cycling, 39, 63, 99, 110
- Nutrient enrichment, 6, 178, 194; exotic species and, 71; in food webs, 33–35, 37, 46, 47, *box* 48–49; fragmentation of habitat and, 88; global environmental change and, 188–201; in marine ecosystems, 136, 140; soil and sediment invertebrates and, 101, 111; in trophic cascades, 39, 41–42, 43. *See also* names of nutrients
- Nutrient loading, 34, 42, 43
- Ocean currents, 113, 131–132, 136, 178, 184
- Ocean dumping, 140
- Ocean floor, 5, 101
- Oceanography, 135
- Oceans, 108, 125–144
- Oenothera parviflora*, 201
- Offshore oil production, 140
- Oil spills, 111, 143, 169
- Omnivory, 35, 131
- Ontogenetic diet shifts, 35
- Open-system dynamics, 33
- Orcas, 136
- Organic matter, 100, 102, 109
- Otolith microchemistry, 135
- Overexploitation, 5, 14, 41, 126; in marine ecosystems, 32, 135, 136, 141, 144
- Overfishing, 137, 138–139, 276
- Oxygenation, 101, 102
- Ozone: stratospheric, 137, 155, 201–202; tropospheric, 176, 196, 197–201, 203
- Ozone hole, 201
- Pacific Islands, 41, 133
- Pacific Ocean, 43, 197, 274
- Packrat middens, 179
- Paleontological data, 135, 139, 179, 182–183
- Paradox of enrichment, 33
- Parasites, 71, 88, 157, 249
- Parent material, 100
- Parkgrass experimental plots, 176, *figure* 177, 195
- Partulidae, 12
- Patches, 85, 227–228, 256
- Pathobiology, 161–163
- Pathogens: ecological health and, 157–164; as exotic species, 66, 67, 71; global environmental change and, 181, 274; soil invertebrates and, 111, 112; testing protocols, 61, 167–168
- PCBs, 136, 140
- Peacock bass, 41
- Pelagic marine communities, 110, 113, 197; food webs in, 35, 39, 40, 42–43, 44, 46

- Penguins, 40
- Pennsylvania, *figure* 177
- Performance evaluation, 235–239
- Periwinkle (*Littorina littorea*), 109
- Permafrost, 100
- Permit compliance, 246
- Persistence of species, 13, 15–19, *box* 21, 40; ecological health and, 158, 164; fragmentation of habitat and, 82, 84, 85, 86–87; global environmental change and, 187; restoration ecology and, 250, 257; sediment invertebrates and, 112–113
- Perturbation, ecological, 2, 276; ecological health and, 164; in food webs, 35, 42, 46–47; human-caused. *See* Human activities; oceanic, 19
- Pesticides, 69, 110, 111, 136, 140
- Pests, 33, 65; biological control of, 34, 44, 48
- Petroleum spills, 136, 140
- Pets, 14, 65
- Phenotypic plasticity, 65
- Phloem feeders, 192
- Phosphorus, 111, 193
- Photosynthesis, 131, 188, 190–191, 194, 200–201
- Phragmites australis*, 66
- Phylogenetic relationships, 114
- Phytoplankton, 35, 42–43, 102, 110, 131, 193, 194, 197, 201
- Pines, 64, 190, 199, 200, 201, 256
- Pink salmon (*Oncorhynchus gorbuscha*), 43
- Pink shrimp, 257
- Pioneer species, 189, 192
- Piscivorous fish, 14, 35, 39, 40
- Planktivorous fish, 14, 35, 39, 41, 43
- Plankton, 40, 50, 129, 130, 135
- Plantago major* populations, 199
- Plant-insect interactions, 50
- Plastics, 136, 140, 277
- Pleistocene, 178–182, 183, 186, 188
- Poaching, 275
- Poison ivy (*Toxicodendron radicans*), 190
- Policy makers, 279; in conservation medicine, 160; decision theory and, 225, 238–239; global environmental change and, 203; marine ecosystems and, 134, 141, 144; research priorities and, 272; in restoration ecology, 248, 254, 256, 259, 262; soil and sediment invertebrates and, 113, 116
- Pollination, 68, 181, 249, 254; fossil pollen, 179, 180, 182; regimes, 71, 88–89
- Pollution, 277–278; ecological health and, 164, 168; exotic species and, 62–63; global environmental change and, 6, 108, 156, 157, *figure* 177, 196, 203, 274; in marine ecosystems, 41, 126, 131–132, 136, 140, 141, 144; in soil and sediment habitats, 102, 110–111; species at risk and, 47
- Polynesia, 12, 15
- Polyploidy, 4
- Ponderosa pines, 256
- Poplar: *Populus grandidentata*, 192, 198; *Populus tremuloides*, 199
- Population dynamics, 32, 64, 70; ecological health and, 158–159, 160, 161–164, 169; in marine ecosystems, 135–136, 138; in restoration ecology, 256
- Population growth, human, 18, 136, 155
- Population viability analysis (PVA), 19, 23, 141, 228
- Positive feedback loops, 87–88
- Power plants, 276
- Prairies, 186, 192, 252, 282
- Prawn production, 137
- Precipitation, 156, 178, 182, 185–186, 253, 274
- Predation effects: in exotic species, 15, 66; in food webs, 32–34, 36, 47; fragmentation of habitat and, 88; global environmental change and, 182, 184; in marine ecosystems, 136, 138, 139; in restoration ecology, 249; in trophic cascades, 39–43
- Predator-prey models, 32–34, 45, 156. *See also* Consumer-resource interactions
- Predators: in biomanipulation, 35; in consumer-resource interactions, 37, 45–46; decision theory and, 228; ecological health and, 156, 162; exotic species as, 59, 66, 71; fragmentation

- Predators (*continued*) of habitat and, 86, 88; global environmental change and, 181; in marine ecosystems, 132; sediment invertebrates and, 109; in trophic cascades, 39–41, 42–44
- Predictions: for exotic species, 60–63, 66–67; for food-web alteration, 42; for GMOs, 68; for restoration ecology, 257–258
- Preservation, 245, 247
- Prey: control of, 39–40, 47; inedible, 35; in trophic cascades, 46
- Primary productivity, 35, 37, 39, 193
- Prochlorophyte picoplankton, 130
- Propagules, 62, 67, 70, 109, 113, 250
- Protected areas, 16, 23, 271–272. *See also* Reserves
- Protein, 109, 126
- Protozoans, 159
- Public health, 157, 159
- Pyrenees, 181
- Quarantine, 60
- Queensland, 182
- Rabies, 157
- Raccoons, 40
- Radiations, evolutionary, 12
- Radioactive waste, 136, 140
- Rainfall patterns, 89, 112, 160, 186, 187; acid rain, 194–197. *See also* Precipitation
- Range size, 15–16, 181–182
- Raptors, 39
- Recessive deleterious alleles, 16
- Reclamation, 247
- Recolonization, 85, 249, 257
- Recovery processes, 248–253
- Recreation, 126, 234
- Re-creation, 247
- Recruitment processes, 33, 35, 89, 183, 191
- Refuges, prey, 33, 112
- Refugia, 180, 181
- Regional planning, 260–262
- Rehabilitation, 247
- Reintroduction of species, 6, 23, 158, 228, 253–254
- Remnant populations, 82, 86, 87–88, 89, 92
- Remote sensing, 278
- Replacement of species, 40, 46
- Reproduction in marine ecosystems, 131
- Reproductive health of species, 156, 188–189, 198, 200
- Research priorities, 3, 7–8, 271–283; for conservation medicine, 161, 164–169, *box* 166–167; for decision theory, 226, 239–241, *box* 241; for exotic species, 60, *box* 72–74; for food-web alteration, 33, 42, 44, 46–50, *box* 48–49; for fragmentation of habitat, *box* 90–91, 92; for global environmental change, 176, 194, 200–201, 203; for marine ecosystems, *tables* 127–128, 132–144, *box* 142–143; for restoration ecology, 246, 248, 257–259, *box* 260–261; for soil and sediment invertebrates, 99, 113–116, *box* 115; for species at risk, 17–24, *box* 20
- “Research Priorities in Restoration Ecology,” 248
- Reserves, 3, 13, 16; designing of, 50, 226–227, 233–235, 274–275; ecological health and, 168; marine, 8, 32, 40–41, 133, 135, 140–142, 144, 272
- Reservoir hosts, 158, 160, 162
- Residuals, 248–249
- Resource allocation theory, 232–233
- Resource supply, 67, 70. *See also* Consumer-resource interactions
- Restoration ecology, 2, 6–7, 245–263, 278; decision theory and, 227–228; exotic species and, 59, 65–66, 67, 69–71, *box* 74; marine, 140, 142–143; soil and sediment invertebrates and, 114
- Restoration Ecology*, 248, 258
- Restoration of Aquatic Ecosystems*, 248
- Retrogression, ecosystem, 178, 195
- Retroviridae, 163–164
- Revegetation, 65, 228, 256
- Reversibility of impacts, 67–68
- Richness: exotic species and, 59; extinction risk and, 4, 17; global environmental change and, 185, 192,

- 195; in marine ecosystems, 131,
133–134, 135; in soil and sediment
habitats, 102, 106, 111, 112
- Riparian systems, 256, 258
- Risk analyses, 229; ecological health and,
160, 162; exotic species and, 70
- RNA viruses, 163
- Rocky intertidal communities, 42,
43–44, 135; food webs in, 46
- Rocky Mountain Biological Laboratory,
184
- Root respiration, 112
- Rothamstead, 176, *figure* 177
- Runoff, 83, 111, 132, 136, 140, 194
- Sage-scrub habitat, 88
- Saipan, 71
- Salinity, 87, 100, 112
- Salmon, 43, 65, 141, 168, 274
- Salt marshes, 109, 125–126, 136–138,
142, 251
- San Francisco Bay, 110
- Santa Barbara, Calif., 248
- Santa Cruz Island, 64
- Satellite imagery, 7, 183
- Scale insect, 251
- Scavengers, 39, 139
- Scientist-citizen, 144
- Scots pine (*Pinus sylvestris*), 200
- Seabirds, 39, 126, 139
- Seafloor communities, 126, 131, 135, 137,
178
- Seafloor drilling, 136
- Seagrass communities, 109, 113, 125,
137, 138, 142–143
- Seal culling, 35
- Sea level, 156, 178, 184
- Seals, crab-eater, 40
- Sea otter–sea urchin–kelp trophic
cascade, 39
- Sea otters, 39, 136
- Sea star (*Pisaster*), 184
- Sea urchins, 39, 41, 139
- Seawater, 129, 131, 193
- Seaweeds, 126, 133, 137
- Sedimentation, 136, 137
- Sediment invertebrates, 99–116, *tables*
104–105, *figure* 107
- Seeding effect, 141
- Seeds: collection of, 66, 254; dispersal of,
249–250; eaters of, 89; nonlocal, 254;
supply of, 70, 71
- Semiarid regions, 186, 187, 189
- Serengeti, 157
- Serology, 162, 165
- Sewage, 37, 111, 136, 140
- Sharks, 40, 131, 139
- Sheep, 88
- Short-grass prairie, 282
- Shrimp farming, 112, 137
- Shrubland, 81, 87, 186, *figure* 187, 189,
193
- Siberia, 181
- Sibling species, 131, 132, 134
- Silicon, 194
- Simian immunodeficiency virus (SIV),
163
- Single-species research, 138
- Sink populations, 88, 132, 227, 276
- in situ* speciation, 5
- Skunks, 40
- Slash-and-burn, 111
- Smelters, 176
- Snails, 12, 126, 196
- Snowmelt, 184
- Snowpack, 184
- Social sciences, 164, 248
- Society for Conservation Biology (SCB),
1–2, 275
- Socioeconomic studies, 142, 238
- Sociopolitical context, 279
- Soil chemistry, 70, 88, 109–111, 114,
196
- Soil compaction, 92
- Soil ecosystems, 192–193
- Soil invertebrates, 99–116, *table* 103,
figure 107
- Soil porosity, 109, 110
- Soil structure, 71, 109–111, 112
- Soil-warming experiments, 184–185,
figure 185, 187
- Solar radiation, 82, 83
- Source-sink theory, 227
- South Africa, 15, 18, 35, 40
- South America, 18, 197
- Southern California, 64, 83, 88, *figure*
199, 251
- Spain, 41, 181

- Spatial scales: in assessment of species at risk, 2, 18–19, 37, 39, 49–50; ecological health and, 157, 158; exotic species and, 63; in fragmentation of habitat, 82, 84, 85, 92; in marine ecosystems, 131, 132, 133, 135, 138; monitoring and, 235; in restoration ecology, 248, 253–254, 256, 257; in soil and sediment habitats, 100, 108
- Spawning, 131, 134, 141
- Speciation rates, 3–4
- Species-area relationships, 133
- Species at risk, 11–24
- Species diversity. *See* Biodiversity
- Spectral analysis, 278
- Spider mites, 199
- Spillover effect, 141
- Spore production, 193
- Sprat, 40
- Sprawl, 277
- Spruce (*Picea critchfieldii*), 179
- Steller's sea cows, 40
- Stingrays, 137
- Stochastic methods, 16, 62, 82, 159, 231
- Stomatal conductance, 198–200
- Storm drainage, 111, 161
- Stressors, 237
- Stress-subsidy theory (Odum), 176, *figure* 177, 178
- Stress tolerance, 69
- Submersibles, research, 132
- Subplot levels, 63
- Subsidies in food webs, 37, 39, 42, 47, 274
- Subsidy-stress gradient (Odum), 176, *figure* 177, 178
- Subtidal marine communities, 139
- Suburban areas, 40, 160
- Succession: in conservation park management, 230–231, *figure* 231; in forest ecosystems, 189–191; in grassland ecosystems, 195, 198; in marine ecosystems, 135; in restoration ecology, 247, 248–250, 253, 254
- Sugar cane, 87
- Sugar maple (*Acer saccharum*), 202
- Survival of species, 182
- Sustainability, 116, 138, 280–281
- Switzerland, 192, 193
- Symbionts, 64, 191, 193
- Systematics, marine, 133
- Tagging, 142
- Tallgrass prairie, 192, 252
- Telemetry, 142
- Temperature: atmospheric, 83, 160, 175, 178–179, 182, 183–185; oceanic, 184, 274; soil, 112, 184–185
- Temporal scales: in assessment of species at risk, 2, 6–7, 18–19, 37, 49–50; in fragmentation of habitat, 85, 87, 92; in marine ecosystems, 131, 133–135, 138; monitoring and, 235; in restoration ecology, 248, 256, 257; in soil and sediment habitats, 108
- Termites, 111
- Thinning, 252
- Threats: deterministic, 82, 85; dynamics of, 17–18, *box* 20–21; to marine biodiversity, 133, 134, 136–140
- Tierra del Fuego, Argentina, 202
- Tigers, 40
- Tillage, 111
- Time lags during invasion, 63–64
- Time scales. *See* Temporal scales
- Top-down effects, 32, 41, 45, 46
- Top-down forces, 33, 34–35, 36–41, *table* 36, 47
- Topography, 100, 182
- Toxicology, 157
- Toxic substances, 155, 169, 176
- Trade, 60–61, 108, 113, 280–281
- Translocation of species, 15, 23, 158
- Transmission of disease, 157–159, 161–163, 168–169
- Transoceanic dispersal, 161
- Trash dumps, 39
- Trawling, 101, 135, 137; bottom, 136
- Trees: global environmental change and, 175, 183; growth rates of, 39, 89; planting of, 88, 250. *See also* names of species
- Trophic cascades, 8, 34–35, 39–41, 42–44, 71, 156; ecological health and, 164; fragmentation of habitat and, 88–89; in restoration ecology, 256
- Trophic levels, 32, 34, 37, 46, 49, 273;

- exotic species and, 67; fragmentation of habitat and, 88; global environmental change and, 186, 192, 194, 196, 199–200; in marine food webs, 131, 138, 197
- Trophic linkages, 131, 135, 182
- Tropical forests, 83, 130; exotic species in, 63; habitat loss and fragmentation in, 4, 81, 188, 274; restoration ecology and, 250; soil and sediment invertebrates in, 111; species at risk in, 14
- Tropospheric ozone, 176, 196, 197–201, 203
- Turkey, 181
- Uganda, 18
- Umbrella species, 237
- Understory vegetation, 83, 190, 198
- United Kingdom. *See* Great Britain
- United States, 23, 59, 68, 110, 198; eastern, 66; midwestern, 88, 111; northeastern, 159; northwestern coast, 39; southeastern, 112, 179, 190; southwest, 183; western, 182, 183
- Urals, 81
- Urban landscapes, 62, 111, 160
- Urban-rural migrations, 18, 282
- Utility theory, 229, 232
- UV-B radiation, 137, 201–202
- Vagility, 249
- Variability, environmental, 16
- Vectors, 59, 61, 159, 160, 169, 182
- Vegetation structure, 83, 111, 252
- Vertebrates: global environmental change and, 181, 192; as hosts, 159; restoration ecology and, 256; terrestrial, 13
- Veterinary medicine, 157, 164
- Vines, 87, 189–191
- Viruses, 67, 131, 159–161, 163–164
- In vitro investigations, 162
- Volatile organic carbon (VOC), 197
- Volcanic habitats, 41
- Wastes, 155; dumping of, 39, 47; radioactive, 136, 140
- Water flow, 100, 110, 112
- Waterfowl, 186
- Water infiltration, 109, 110
- Watersheds, 50, 110, 246, 282
- Water table, 87
- Weediness, 68–69
- Weeds, 88, 195, 201
- Weedy vines, 87, 189–191
- West Nile virus (WNV), 159–161
- Wetlands, 101, 112, 126, 194, 256, 257
- Whales, 39, 40
- Wheatbelts, 81, 87–88, 89, 92
- White abalone, 136
- White-footed mice (*Peromyscus leucopus*), 156
- White oak (*Quercus alba*), 180, 192
- White Oak Plantation workshop, 2
- White spruce (*Picea mariana*), 183
- White-tailed deer (*Odocoileus virginianus*), 156
- Whole-ecosystem studies, 184–185, 202
- Wildlife, 66, 158, 159, 161–164, 165, 168–169, 277. *See also* names of species
- Wog Wog, Australia, 83
- Wolves, 39–40
- Wood-boring gribble (*Limnoria tripunctata*), 62
- Wood ducks, 252
- Woodland, 81, 87, 88
- World War II, 71
- Wyoming, 158
- Yellowstone National Park, 162–163
- Zebra mussel (*Dreissina polymorpha*), 7, 110
- Zoning, 235
- Zoonotic pathogens, 159, 160, 163
- Zooplankton, 35, 39, 41, 43, 131, 183

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